SYSTEMATICS OF THE SOUTHERN AFRICAN GENUS *HEXAGLOTTIS* (IRIDACEAE—IRIDOIDEAE)[1]

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ABSTRACT

Hexaglottis is a genus of six species occurring along the west and south coast of southern Africa, an area of predominantly winter rainfall. It is a member of tribe Irideae subtribe Homeriinae, which is characterized by a cormous rootstock and secondarily bifacial leaves. *Hexaglottis* is defined largely by an unusual flower structure with shortly clawed subequal tepals and completely divided filiform style arms. This revision includes three new species, *H. namaquana, H. riparia,* and *H. brevituba,* and three that were described before 1800. On the basis of chromosome cytology, experimental hybridization, and vegetative morphology, *H. nana* is excluded from *Hexaglottis*; it is probably allied to the genus *Rheome.* The relationships and history of *Hexaglottis* are discussed, and, following a detailed presentation of taxonomically important characters including chromosome cytology, *Hexaglottis* is analyzed cladistically. *Hexaglottis namaquana* is suggested to be an isolated and primitive relict and the sister species of the remainder of the genus. The southern African genus *Homeria* is probably the closest ally and sister group of *Hexaglottis.* The putative ancestry of these two genera is traced back to a group of species of *Moraea* section *Moraea.* Basic chromosome number in *Hexaglottis* is $x = 6$, while *H. nana* has $x = 10$, a number shared with *Rheome* and basic for *Moraea.*

Hexaglottis is a small genus of Iridaceae tribe Irideae restricted to the winter rainfall area of southern Africa (Fig. 1). It has linear, bifacial, and usually channeled leaves; corms of the *Moraea* type composed of a single swollen internode and apically rooting bud; and umbel-like inflorescence units (rhipidia) enclosed in large, opposed, herbaceous bracts (spathes). This series of characteristics establishes its systematic position in the predominantly southern African subtribe Homeriinae (Goldblatt, 1976b: 661, 1980) of the Old World tribe Irideae. The floral structure is distinctive and, although not unique, defines the genus. The subequal tepals have short erect claws and horizontally extended limbs, and the styles are short with branches divided almost to the base into paired filiform arms that extend outwards on either side of the subtending anther. The flowers are yellow and fugacious, lasting only a few hours. Additional features are firm, brown- to blackish-reticulate corm tunics and a basic chromosome number of $x = 6$.

Moraea hexaglottis (Goldblatt, 1986) has a similar flower structure, but the flowers are blue, unlike *Hexaglottis,* and the basic chromosome number is $x = 10$. A second species, described by H. M. L. Bolus as *H. nana,* has flowers essentially identical to those of other species of *Hexaglottis,* but it has dark brown, unbroken corm tunics, unusual fasciculate rhipidia, and a base number of $x = 10$. It is here excluded from *Hexaglottis.* Crossing studies, chromosome morphology (detailed below), and vegetative morphology indicate that it is related to the small genus *Rheome,* comprising *R. maximiliani* and *R. umbellata,* and probably also to *Moraea linderi* and *M. margaretae,* which recent unpublished investigation has indicated are closely allied to *Rheome.*
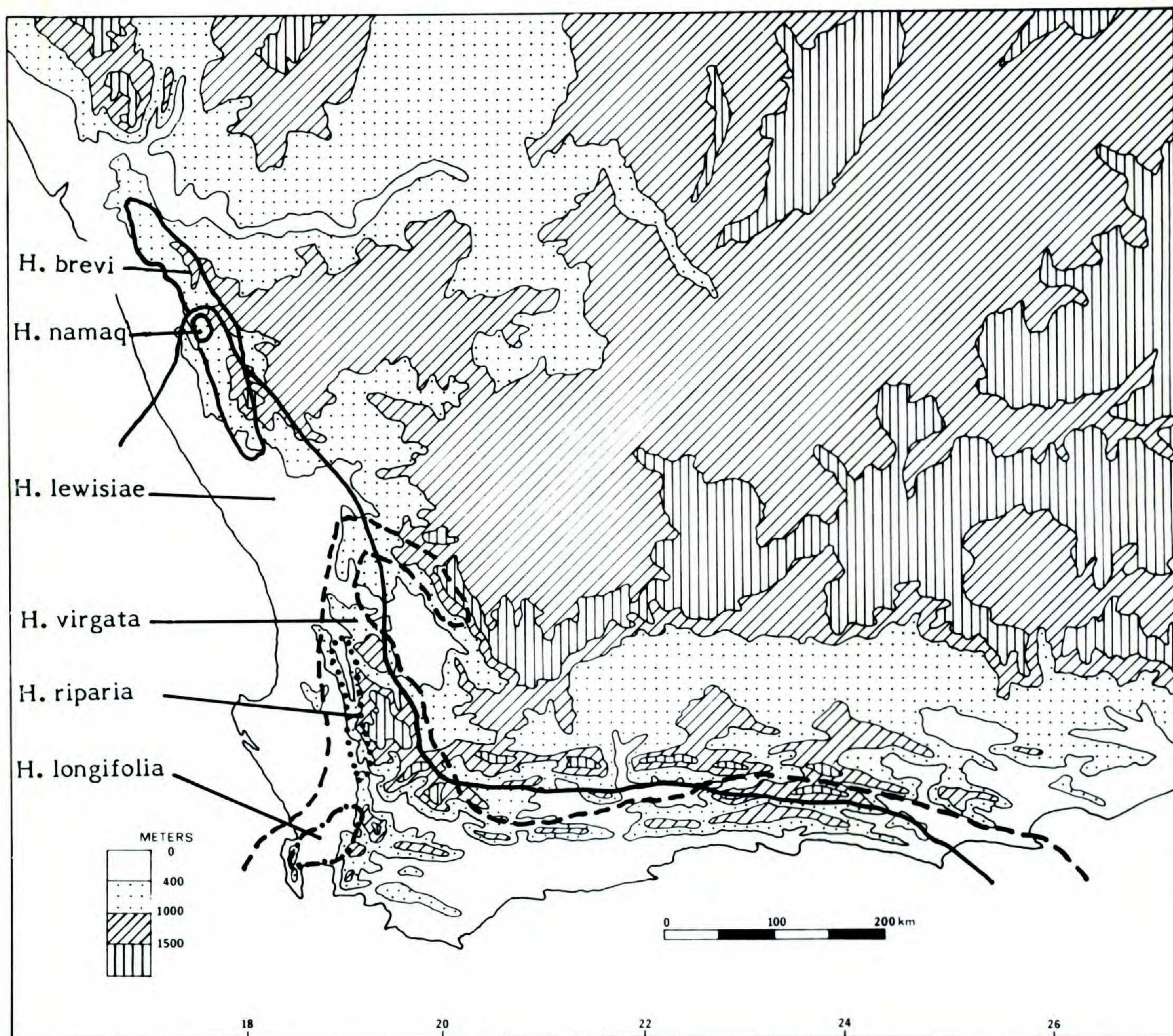
The peculiar *Hexaglottis* type of flower is thus believed to have evolved independently three times. It defines *Hexaglottis* only in combination with the vegetative and chromosomal features mentioned above.

RELATIONSHIPS

Hexaglottis is probably most closely allied, within the Homeriinae, to *Homeria,* and avail-

FIGURE 1. Geography of *Hexaglottis*.

able morphological and cytological data suggest that the two genera have as a common ancestor (Fig. 5) probably a species or group of species of *Moraea* allied to *M. flexuosa* (Goldblatt, 1982). The characteristics that *Homeria* and *Hexaglottis* share include subequal tepals, the claws of which cup the lower part of the filaments, and style branches reduced from the elaborate flattened structures basic for Homeriinae (Goldblatt, 1980, 1986) and probably for the entire tribe Irideae (Goldblatt, in prep.). The two genera also share a similar and derived karyotype with $x = 6$ comprising strongly acrocentric to subacrocentric chromosomes. Genome size (Goldblatt et al., 1984) is similar, 22–29 pg DNA in *Homeria* and 20.6 pg DNA in *Hexaglottis namaquana*, the only species of the genus for which this is known. *Moraea flexuosa* has a comparable karyotype. Other members of *Moraea*

that appear less closely related include a part of the heterogeneous section *Moraea*, $x = 10$, and section *Polyanthes*, $x = 6$, the latter distinguished by having blue to violet flowers (a derived condition in *Moraea*). The karyotype in section *Polyanthes* is also somewhat different in comprising acrocentric and submetacentric chromosomes (Goldblatt, 1980).

HISTORY OF *HEXAGLOTTIS*

The taxonomic history of *Hexaglottis* has been described by G. J. Lewis (1959) in detail, and it is reviewed here briefly. The first of the species now admitted to *Hexaglottis* was described by Nicholas Jacquin in 1776 as *Ixia longifolia*. The excellent figure that now serves as the type of the species is unmistakably this Cape Peninsula species, often confused with the more common and widespread *H. lewisiae*. Shortly afterward,

the younger Linnaeus described a second species as *Moraea flexuosa* (Linnaeus fil., 1781). This name is now regarded as nomenclaturally superfluous and illegitimate, and a new name, *H. lewisiae*, was proposed for the species in 1971 (Goldblatt, 1971a) (see discussion under this species).

The very distinctive, late-flowering *Hexaglottis virgata* was described in 1791 by Jacquin, this species also being assigned to *Moraea*. As with Jacquin's earlier species of *Hexaglottis*, a fine illustration leaves no doubt about its identity. Thus, all three common southwestern Cape species of the genus were known and described by the beginning of the nineteenth century when E. P. Ventenat erected the genus in 1808. Ventenat made no transfers to his new genus, mentioning only *Ixia longifolia* Jacq. by name, "*Ixia longifolia* Jacq. etc.," which leaves one wondering whether he had further species in mind. The genus soon gained acceptance, and combinations were made for *H. longifolia* by R. A. Salisbury (1812) and for *H. virgata* and the illegitimate *H. flexuosa* by Sweet (1830). One more species was collected in the nineteenth century, *H. riparia*, discovered by C. F. Ecklon & C. L. Zeyher (their *Irid. 30*), but the collection was consistently assigned to *H. flexuosa*.

The three described species of *Hexaglottis* were regarded as a single taxon by Klatt (1866) under the name *Homeria spicata* (Ker) Sweet, the type of which is conspecific with the earlier *Homeria elegans* (Jacq.) Sweet (Goldblatt, 1981). Later, Klatt (1882: 52, 1895: 159) recognized *Hexaglottis* with *H. longifolia* (including *H. lewisiae*) and *H. virgata*. Baker's (1896) definitive nineteenth century floristic treatment of the Iridaceae in *Flora Capensis* is identical, but he understood *Hexaglottis* so inadequately (Lewis, 1959) that his work on the genus must be disregarded.

Louisa Bolus added one more species to *Hexaglottis* in 1932, the west coast *H. nana*, which, although common, was apparently only discovered in the 1920s. *Hexaglottis nana* as already outlined differs markedly in its vegetative morphology, cytology, and crossing relationships from *Hexaglottis* and is now excluded from the genus (for comparison of *H. nana* with *H. lewisiae* see Fig. 2).

Lewis's (1959) revision of *Hexaglottis* admitted four species to the genus and two new varieties, *H. virgata* var. *lata* and *H. longifolia* var. *angustifolia*, neither of which is recognized here.

Collecting since the publication of Lewis's revision, especially in the arid country to the north of the Cape Floristic Region, has substantially expanded the knowledge of *Hexaglottis*. I discovered a new species, *H. namaquana*, in the Spektakel Mountains of northern Namaqualand in 1974 and extended the range of *H. lewisiae* into these mountains west of Springbok. The distinctive new *H. brevifolia* of northern Namaqualand and the Richtersveld is now recognized, specimens previously having been placed in *H. lewisiae* and *H. virgata* by Lewis, and a new subspecies of *H. virgata*, subsp. *karooica*, has been described from the Roggeveld Escarpment in the western Karoo. Lastly, plants treated as *H. longifolia* var. *angustifolia* by Lewis (1959) have been re-collected and are regarded as a distinct species described here as *H. riparia*.

The picture in 1959 of *Hexaglottis* as a small genus essentially of the Cape Floristic Region with minor extensions of *H. lewisiae* and *H. virgata* to the north into semi-arid Namaqualand has changed fundamentally. *Hexaglottis* must now be viewed as centered along the interior Cape West Coast with extensions south and east into the Cape Floristic Region.

MORPHOLOGY

Rootstock. Species of *Hexaglottis* have a corm of the *Moraea* type (Goldblatt, 1976b: 670, 1981: 428) consisting of a single swollen internode with an apical primordium from which both shoot and roots are produced. This organ is one of the two major specializations defining subtribe Homeriinae. The corm originates from an axillary bud near the base of the flowering stem. The corm tunics are basically like those found in *Homeria* and several species of *Moraea* subgenus *Moraea* and consist of a coarse open network of hard, wiry, dark brown to black fibers. In *Hexaglottis* the mealy substance between the fibers often persists and clings to the fibers, imparting a lighter color to them. The outer tunic layers are usually paler in color and characteristically medium brown in many collections of *H. virgata* and *H. lewisiae*. The two moisture-loving species, *H. riparia* and *H. longifolia*, have softer-textured tunics, the outer layers of which become light brown and the fibers are relatively fine.

Leaves. The leaves are bifacial with a sheathing base and more or less linear and channeled, this being the basic leaf type for Homeriinae. The leaves of *Hexaglottis namaquana* are the most distinctive, being relatively broad, almost prostrate, strongly undulate, lightly twisted with the
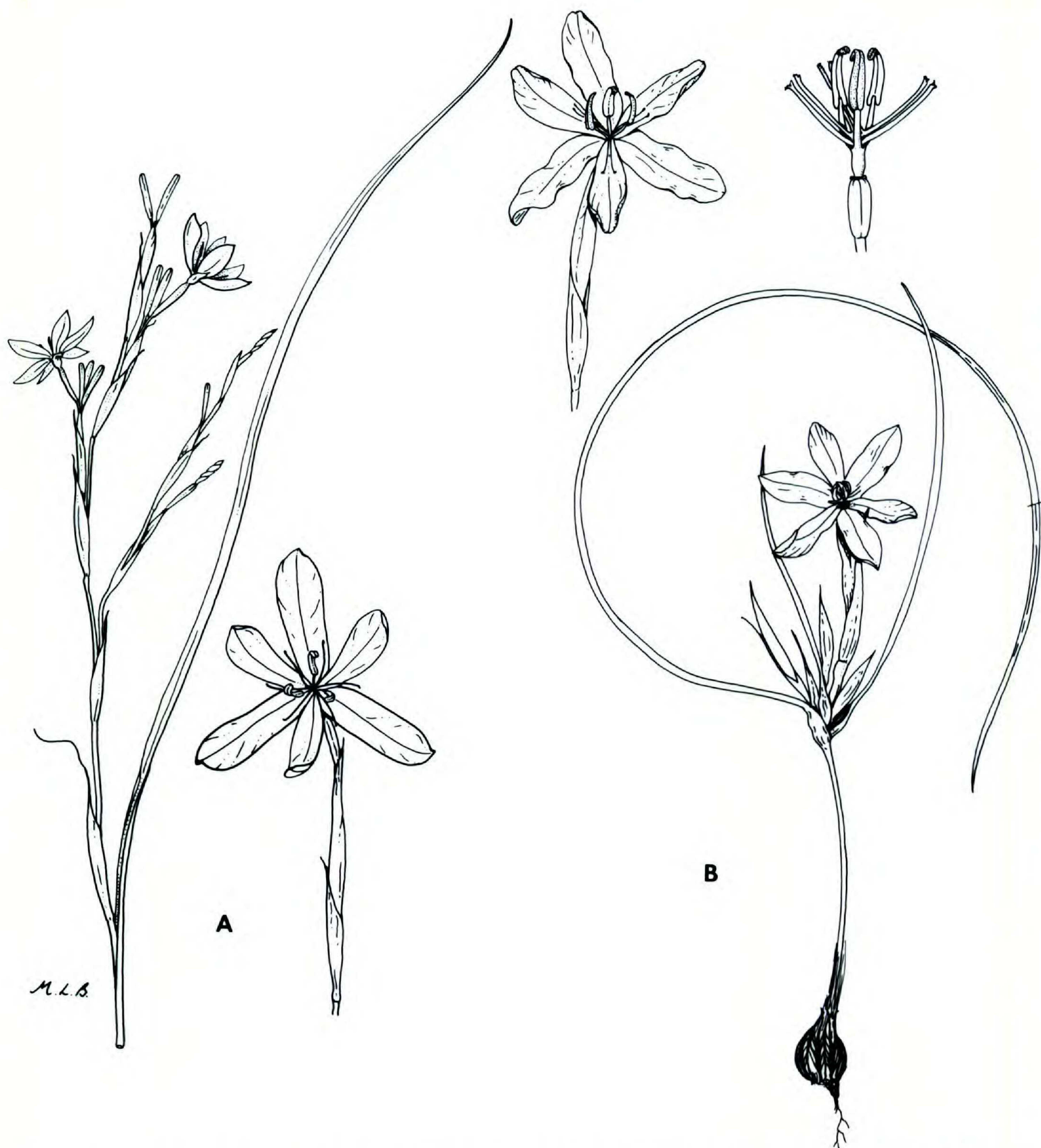
FIGURE 2.   Habit and flowers of *Hexaglottis lewisiae* (A) and for comparison the vegetative and floral morphology of *'Hexaglottis' nana* (B). Compare for example, Figures 6 and 11. Habits ×0.5; single flowers full size; separated stamens and style branches ×2.

margins sometimes somewhat crisped. The leaf condition in *H. namaquana* must be regarded as derived from the much more common erect linear leaf with straight margins found in the other species of the genus and thus represents one or possibly two autapomorphies. The leaves of *H. virgata* may be lightly coiled distally, a feature obscure in herbarium material. There are usually two to three foliage leaves per plant, but the number depends on growing conditions, so that fewer

leaves are produced in drier seasons. Plants always produce more leaves in the greenhouse than in the wild. Under optimal conditions *H. longifolia*, *H. riparia*, and *H. virgata* subsp. *karooica* have four or five leaves. The leaves are inserted fairly close together near or slightly below ground level, but in *H. lewisiae* subsp. *secunda*, the leaf or leaves may be inserted some distance above the ground.

Flowering stem, sheathing bract leaves, and

branching patterns. The flowering stem is more or less erect, particularly so in *Hexaglottis virgata,* but willowy and nodding in *H. longifolia* and *H. riparia.* There may be up to three or four major branches, each stalked and bearing a few to several sessile lateral rhipidia (the inflorescence units). The exception is *H. namaquana* in which all the rhipidia are stalked, presumably the ancestral condition, and thus terminal on the main or lateral branches. The sessile lateral rhipidia are a derived feature, and a synapomorphy separating the main group of species of *Hexaglottis* from *H. namaquana.*

A sheathing bract leaf with a closed sheath subtends each branch or lateral rhipidium. In the latter, the sheathing bract leaf resembles the inflorescence spathes, which it may completely conceal. Each sheathing bract leaf generally overlaps the one above, except in *H. longifolia,* the cauline internodes of which are comparatively long. Lewis (1959) used this feature as an important character for distinguishing *H. longifolia.*

Rhipidia. The inflorescence units are of the basic type for Iridaceae, consisting of compressed cymose umbels enclosed in two large, opposed, sheathing spathes, the inner of which exceeds the outer except in the lateral rhipidia of *H. longifolia,* where they are nearly equal, a presumably specialized condition. Individual flowers are pedicellate and subtended by a single membranous bract contained within the spathes. The flowers are produced serially, a few days apart, at which time the pedicels elongate to raise the flowers out of the spathes. In *Hexaglottis brevituba* and *H. virgata* the pedicels are short and the ovaries are included in the spathes, but the flowers have a perianth tube that serves the same function as the pedicel in extending the flowers beyond the spathes. The spathes are initially herbaceous with dry attenuate apices, but towards the middle of the flowering season they begin to dry out and become light brown and chaffy towards the middle. The short pedicels, included ovaries, and perianth tube are important synapomorphies separating *H. brevituba* and *H. virgata* from the rest of the genus.

Flower. The flower is almost uniform throughout *Hexaglottis,* except for the presence of a tube in *H. brevituba* and *H. virgata,* and is unusual in Iridaceae in the structure of the style and style branches and the relationship of the latter to the stamens. The shortly clawed tepals are pale to deep yellow and subequal, or those of the inner whorl are slightly smaller. The claws, 1–2 mm long, are erect and form a cup around the base of the filaments, while the relatively long limbs spread horizontally. The filaments are united below for 1–3 mm into a column, at the apex of which the style divides into three branches, each opposite a stamen. The branches divide almost immediately to form two long, filiform, apically stigmatic arms which extend outwards more or less horizontally to either side of the subtending stamen. The flowers are short-lived, opening in the mid to late afternoon and fading about three hours later. The unusual structure of the style of this flower has led to the placement of all species with this character together in a single genus, but data presented in this revision indicate that *H. nana,* described by Louisa Bolus in 1932, is distantly related to the other species of *Hexaglottis* and must have acquired its *Hexaglottis*-like flower by convergence. A similar flower has also evolved in *Moraea hexaglottis* (Goldblatt, 1986). The divided style branches and filiform ascending arms are the primary characters separating *Hexaglottis* from other genera of Homeriinae, to which should perhaps be added the partly free filaments, a probable reversal from an ancestral condition with apically free filaments as in the putative relatives *Moraea flexuosa* and *Homeria* (Fig. 5). The free part of the filaments allows the long anthers to be displayed prominently and also well separated from the style branches which almost always in Homeriinae divide at the top of the united part of the filaments.

As already mentioned in the paragraph dealing with rhipidia, flowers of *Hexaglottis virgata* and *H. brevituba* have short pedicels and included ovaries. In other species the pedicels are about as long as the spathes, and at anthesis the ovary is almost always exserted.

Fruit. Capsules of *Hexaglottis* species vary considerably and are important in recognizing species and in assessing phylogenetic relationships. The capsules are typically exserted from the spathes and are basically ellipsoid in shape, as in *H. namaquana* and *H. lewisiae* subsp. *secunda.* In the latter, the capsule has a short beak, a feature not always evident in populations from Namaqualand but strongly expressed in plants from the northwest Cape. *Hexaglottis lewisiae* subsp. *lewisiae* has trigonous, more or less cylindric capsules, while obovoid to clavate capsules distinguish *H. riparia* and *H. longifolia.* The capsules of *H. longifolia* are relatively large, 12–16 (–23) mm long, but only 6–10(–12) mm long in *H. riparia,* the smaller size presumably basic and consistent with capsule dimensions of other

TABLE 1. Chromosome numbers in *Hexaglottis* and *Rheome*. Original counts are marked with an asterisk. Previous counts were reported by Goldblatt (1971b, 1980).

Species	Haploid Number	Collection Data
		HEXAGLOTTIS
H. namaquana Goldbl.	6*	Spektakel Pass, west of Springbok, *Goldblatt 3059* (MO).
H. lewisiae Goldbl.		
subsp. *lewisiae*	6*	Tulbagh Cemetery, *Goldblatt 5224* (MO); Cape Town, Kirstenbosch Gardens (wild plants), *Goldblatt 5104* (MO).
subsp. *secunda* Goldbl.	6	Loeriesfontein road, north of Nieuwoudtville, *Goldblatt 108* (J).
	6*	Spektakel Pass, west of Springbok, *Goldblatt 6513* (MO); granite outcrops SW of Skuinskraal, near Hondeklipbaai, *van Berkel 453* (MO); near Nieuwoudtville, *Goldblatt 6535* (MO).
H. riparia Goldbl.	6*	Olifants R. bank at Citrusdal, *Goldblatt 6555* (MO).
H. longifolia (Jacq.) Sweet	12*	Cape Town, Kirstenbosch Gardens (wild plants), *Goldblatt 5934* (MO), *Malan 120* (NBG).
H. brevituba Goldbl.	12*	Near the Kosies road, NW of Steinkopf, *Goldblatt 5748* (MO).
H. virgata (Jacq.) Sweet		
subsp. *virgata*	5	Signal Hill, Cape Town, *Goldblatt 71* (J).
	5*	Slopes near parking area, Signal Hill, Cape Town, *Goldblatt 6747* (MO); Signal Hill, near Sheik's tomb, *Goldblatt 6768* (MO); lower slopes of Devils Peak, *Goldblatt 6717* (MO).
	6*	Hills west of Riversdale, *Goldblatt 5436* (MO); Franskraal, near the coast, *Goldblatt 5368* (MO); near Misgund, *Goldblatt 6792* (MO); between Bredasdorp and Napier, *Goldblatt 6937* (MO); between Doorn River and Bidouw road, *Goldblatt 5941* (MO).
subsp. *karooica* Goldbl.	7*	Roggeveld, near Voelfontein farm, *Goldblatt 6336* (MO); Blomfontein farm west of Middelpos, *Snijman 765* (MO, NBG).
'Hexaglottis' *nana* L. Bolus	10*	Olifants River valley near Alpha, *Goldblatt 5120* (MO); Pakhuis Pass, near Soldaat Kop, *Goldblatt 5158* (MO).
		RHEOME
R. maximiliani (Schltr.) Goldbl.	10	Brandewyn River near Travellers Rest, *Goldblatt 3884* (MO).
R. umbellata (Thunb.) Goldbl.	10*	East end of Du Toits Pass, *Goldblatt 5907* (MO).
	15	Paarl Golf Course, *Goldblatt 4414* (MO).
	15*	Piketberg, top of Versveld Pass, *Goldblatt 5163* (MO); foot of the Elandskloof Mts. at Elandsberg farm, *Goldblatt 5853* (MO).

species. The capsules of *H. virgata* and *H. brevituba* are included in the spathes and are narrowly fusiform. They remain enclosed by the spathes through ripening and dehisce only in the upper part.

The seeds are brown and basically angular, but elongate in *H. virgata* and *H. lewisiae* subsp. *lewisiae*, both of which have narrow capsules (seeds of *H. brevituba* are not known). Seeds of *H. longifolia* are unusually large, a feature possibly relating to its polyploid state. *Hexaglottis lewisiae*

subsp. *secunda* can usually be distinguished by the raised and winglike angles of the seeds. The seeds are known from only a few populations of this subspecies, and I hesitate to regard the winglike angles as characteristic of the taxon until more is known about their occurrence.

CHROMOSOME CYTOLOGY

The cytology of *Hexaglottis* was investigated extensively for this study. The method followed here is the same as that outlined for similar in-
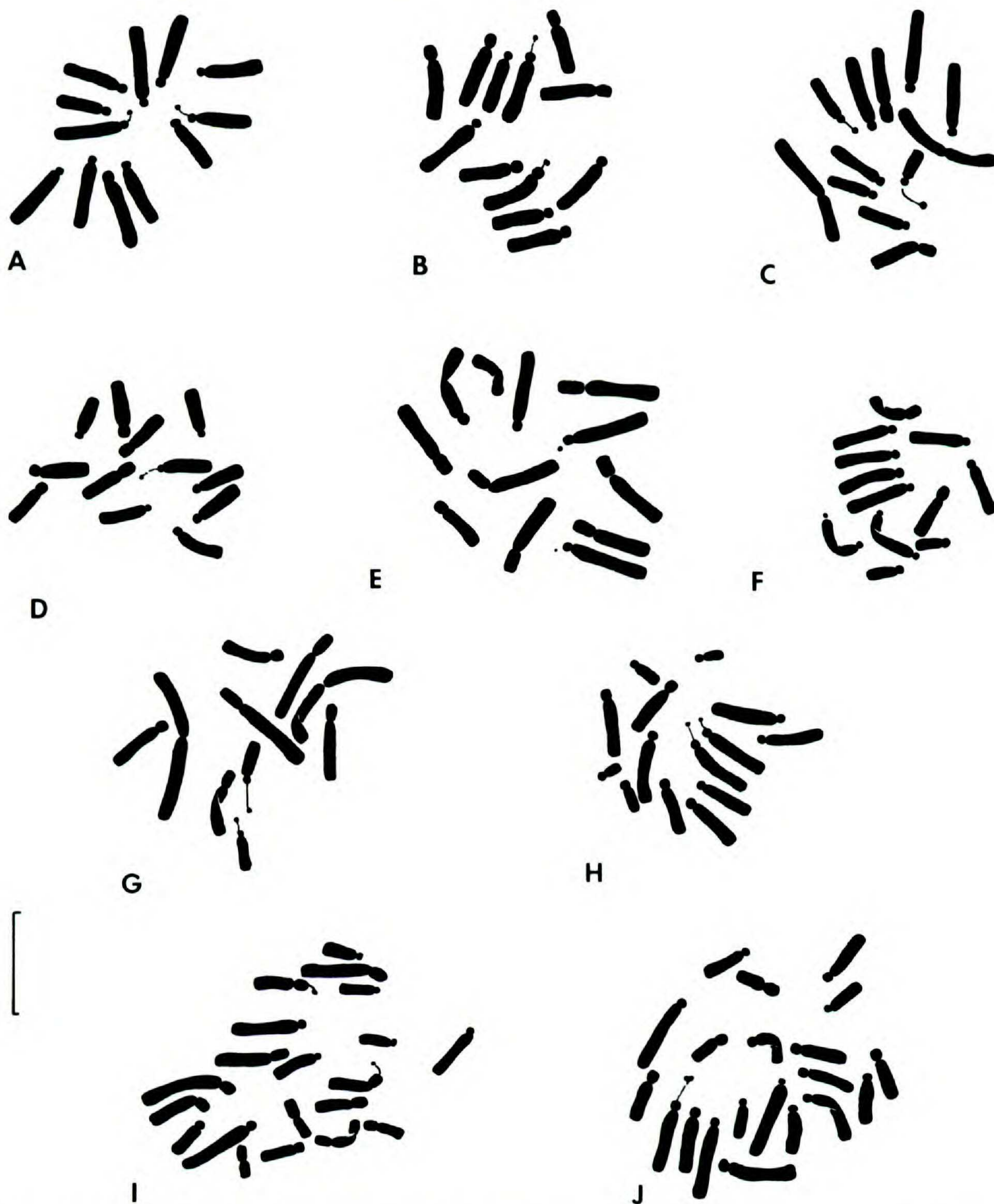
FIGURE 3.   Mitotic metaphase configurations of *Hexaglottis* species.—A. *H. namaquana.*—B. *H. lewisiae* subsp. *lewisiae.*—C. *H. lewisiae* subsp. *secunda.*—D. *H. riparia.*—E. *H. virgata* subsp. *virgata,* $2n = 12$ (Franskraal, *Goldblatt 5368*).—F. subsp. *virgata* $2n = 12$ (Doorn R.–Bidouw, *Goldblatt 5941*).—G. subsp. *virgata* $2n = 10$ (Signal Hill, *Goldblatt 6747*).—H. *H. virgata* subsp. *karooica,* $2n = 14$.—I. *Rheome umbellata,* $2n = 20$.—J. '*Hexaglottis*' *nana,* $2n = 20$. Scale $= 10 \mu$m.

vestigations in Iridaceae (Goldblatt, 1979, 1980). The results are presented in Table 1. Base number in *Hexaglottis* is $x = 6$, this originally suggested on the basis of one count for *H. lewisiae* (as *H. flexuosa*), $2n = 12$ (Goldblatt, 1971b), while a single count for the specialized *H. virgata,* $2n = 10$, suggested that this species was a derived aneuploid. Several additional counts for *Hexaglottis* have confirmed $x = 6$ as basic. *Hexa-*

glottis lewisiae, H. namaquana, H. riparia, and three populations of *H. virgata* all have $2n = 12$. The two known populations of *H. virgata* subsp. *karooica* both have $2n = 14$, while *H. longifolia* is tetraploid with $2n = 24$.

The two populations of *Hexaglottis nana* examined cytologically were found to have a diploid number of $2n = 20$ and a karyotype exactly like that of the diploid *Rheome maximiliani*

(Goldblatt, 1980). Basic chromosome number in *Rheome*, already established (Goldblatt, 1980) as $x = 10$, has been confirmed here, with additional counts for *R. umbellata*. This species was originally thought to be triploid, $2n = 30$, but one diploid population has been discovered, as well as two more triploid populations (Table 1).

The chromosomes of *Hexaglottis* species are fairly large, ranging in size in the basic karyotype from 5 to 9 μm with the method used here. The basic karyotype as exemplified in the least specialized species, *H. namaquana*, consists of acrocentric to nearly telocentric chromosomes with a satellite on the distal end of the short arm of the third or fourth longest pair (Fig. 3A).

Hexaglottis lewisiae subsp. *lewisiae* and *H. riparia* (Fig. 3B, D) have a similar karyotype, but the satellite is located on one of the longest chromosome pairs. Size differences are relatively small, and the shortest chromosomes are only ±35% smaller than the longest (Fig. 3A–C; see also Goldblatt, 1971b: 364, fig. 14E). *Hexaglottis longifolia* is tetraploid, $2n = 24$, but otherwise has a karyotype comparable to that of *G. riparia* and *G. lewisiae* subsp. *lewisiae*.

The Namaqualand populations of *Hexaglottis lewisiae* subsp. *secunda* (Fig. 3C) have an apparently derived karyotype. The longest chromosome pair is metacentric and about 12.5 μm long, nearly twice as long as the next in size, an acrocentric pair. The third or fourth pair is submetacentric, while the smallest pair has a large satellite (Fig. 3C) and is only 5 μm long, about one-third as long as the long metacentric. This karyotype has been found in two widely separated Namaqualand populations of this poorly sampled subspecies (Table 1), but a population from Nieuwoudtville, well to the south, has a karyotype of acrocentric chromosomes, unusual only in having a satellite on the end of a long arm of a long chromosome pair. The single plant that I examined was structurally heterozygous, having only one satellite present.

In the specialized *Hexaglottis virgata*, there is unexpected intraspecific variation in the karyotype. The presumed basic karyotype (Fig. 3E) as found in southern Cape populations of subsp. *virgata* consists of six pairs of acrocentrics, the first and third of which have a distinctly longer short arm. The satellite is located on the second longest and strongly acrocentric pair. A northern population of *H. virgata* (*Goldblatt 5491*) can be distinguished cytologically by having satellites on the distal end of the long arm of the longest

and strongly acrocentric pair (Fig. 3F). The northern populations may be a separate cytological race, but more material needs to be examined. Cape Peninsula populations of *H. virgata* are aneuploid, $2n = 10$ (Goldblatt, 1971b), and have a karyotype exhibiting considerable structural rearrangement. The longest pair (Fig. 3G) is metacentric and about 12 μm long, while unusually large satellites are located on the shortest and acrocentric pair, the satellite being longer than the short arm. Robertsonian fusion of two acrocentric, medium-sized pairs and the translocation of the satellite to the smallest pair would account for the modified karyotype.

Hexaglottis virgata subsp. *karooica* is unusual in the genus in its diploid number of $2n = 14$ (Fig. 3H). Three individuals of both known populations were examined. The chromosomes are more strongly acrocentric than in the basic $2n = 12$ cytotype of subsp. *virgata* and there are two, rather than a single, small pairs. The origin of the extra small pair is unknown. Satellites in the subspecies are located on the ends of the short arms of a large chromosome pair.

Karyotype evolution in *Hexaglottis* appears to have proceeded from a basic, rather uniform, acrocentric set of chromosomes to increasing symmetry with the development of greater size differences and, in *H. lewisiae* subsp. *secunda* and the Cape Peninsula populations of *H. virgata* subsp. *virgata*, the evolution of large metacentrics, in the latter with a decrease in base number to $x = 5$. *Hexaglottis virgata* subsp. *karooica* seems to be one of the rare examples in Iridaceae of an increase in base number, as the karyotype of this specialized and rare taxon is almost certainly derived from ancestors with $x = 6$. The origin of the extra pair of small chromosomes is problematic. The tetraploid *H. longifolia* may have evolved by amphipolyploidy, and its large size, especially in vegetative and fruit characters, may be a direct result of its polyploidy. *Hexaglottis brevifolia* has the same base number as the genus but details of its karyotype were not seen in the poor material available.

HYBRID STUDIES

A crossing program involving three species of *Hexaglottis*, *H. nana*, and *Rheome maximiliani* in the spring of 1982 produced results (Fig. 4) that confirm the indications from cytology that *H. nana* is allied to *Rheome* rather than to *Hexaglottis*. *Rheome maximiliani* could be crossed readily to emasculated flowers of *H. nana*, while
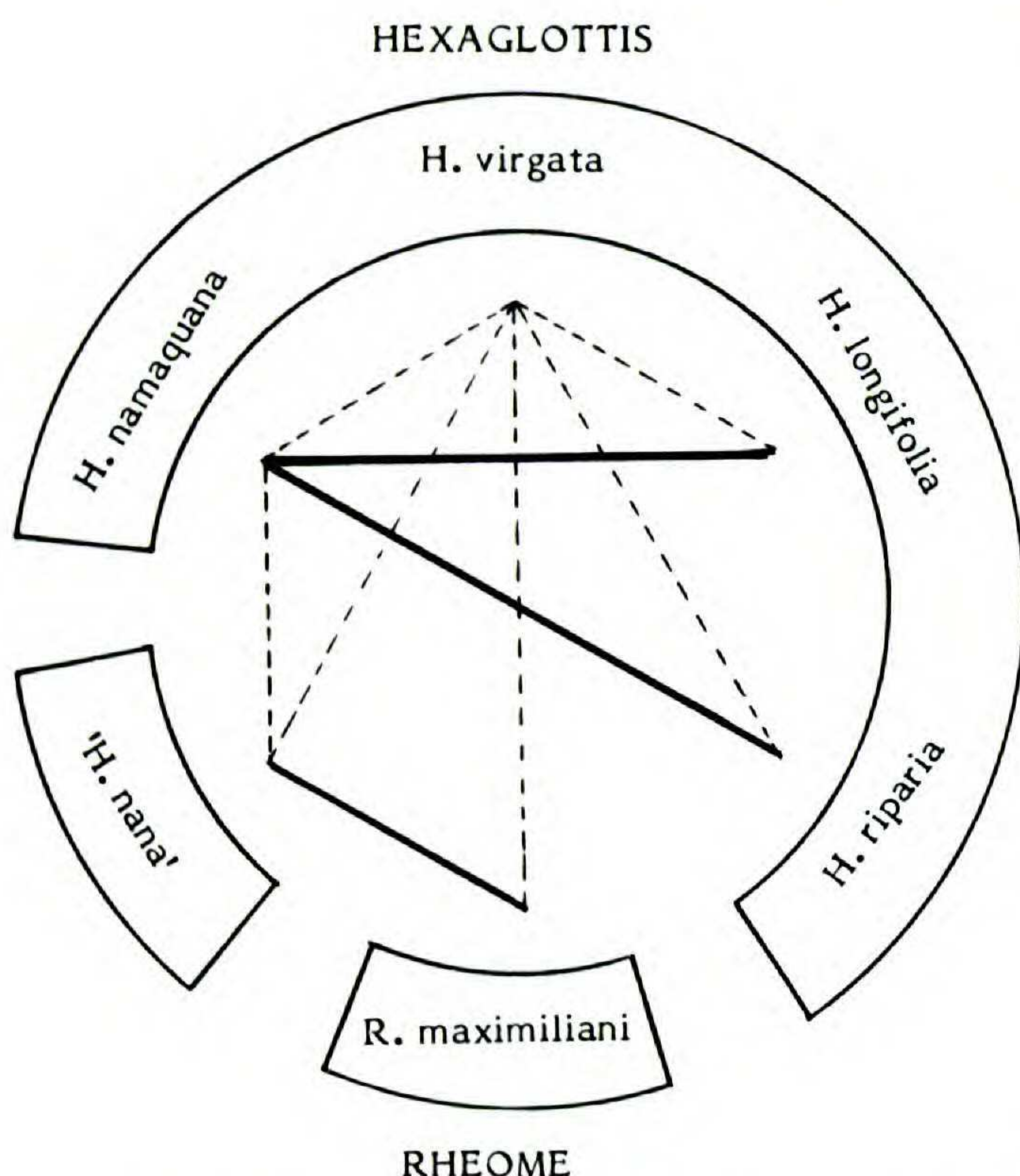
HEXAGLOTTIS

FIGURE 4. Crossing relationships in *Hexaglottis,* '*H.*' *nana,* and *Rheome maximiliani.* Heavy lines indicate successful crosses; dotted lines indicate crosses were attempted but failed.

repeated attempts to cross both of these species with three species of *Hexaglottis* used in the study failed. Attempts to make interspecific crosses between other species of *Hexaglottis* produced mixed results. Successful crosses were made between *H. longifolia, H. riparia,* and *H. namaquana,* but all attempts to cross *H. virgata* with these species failed. The study was not extended to the species of *Moraea* that are most similar to *Rheome,* namely *M. linderi* and *M. margaretae,* as neither was available in cultivation.

REPRODUCTIVE BIOLOGY AND POLLINATION

The *Hexaglottis* flower is relatively small and inconspicuous, especially for Iridaceae, but as plants typically grow in fairly dense colonies and produce several flowers each day, they often make an effective display. Individual flowers of all species last only a few hours, opening at constant times depending on the species or population, in mid to late afternoon and closing in the early evening. All species except *H. longifolia* are strongly self-incompatible (*H. brevifolia* unknown). Very rarely a few undersized capsules are produced on plants by autogamy late in the flowering season, but normally flowers do not set seed by their own pollen, even though a small

quantity of pollen is usually deposited on the stigmas while the flowers are open. The exception, *H. longifolia,* is self-compatible and autogamous. Plants produce numerous full capsules with fertile seed without cross-pollination.

The pale to deep yellow stellate flowers of *Hexaglottis* are typically pollinated by bees. The small nectaries, located at the base of the outer tepals, produce a limited quantity of nectar which is retained in the space between the short, erect tepal claws and the filaments. The nectar, however, seems to be of secondary importance, and the insect visitors appear to be attracted primarily to the pollen, a large amount of which is produced in the relatively long anthers.

Although the flowers of all species are very similar, there is a considerable difference in the response of bees to the flowers of the three species, *H. lewisiae, H. virgata,* and *H. longifolia,* for which I have careful observations. *Hexaglottis longifolia* is totally unattractive to bees, which ignore open flowers even when they pass close to them. The same bees, however, visit the opening flowers of *H. lewisiae* subsp. *lewisiae* growing within a few meters of *H. longifolia.* Bees gather around populations of *H. lewisiae* in the middle of the afternoon about the time its flowers normally open, and they begin to gather pollen as soon as the flowers open.

Hexaglottis virgata is similarly attractive to bees, but pollinator activity was always less intense than in *H. lewisiae.* Honeybees (Apidae) and species of Anthophoridae were observed pollinating *Hexaglottis* flowers.

PHYLOGENY

Cladistics affords the most objective and critical method of assessing the phylogeny of a group, and the results of a cladistic analysis of *Hexaglottis* and its immediate allies are presented below. The cladogram (Fig. 5) was constructed manually following concepts of clustering by shared derived characteristics (synapomorphies) and parsimony established by Hennig (1966) and adapted by several botanists recently (Bremer, 1976; Humphries, 1981; Funk, 1982; Goldblatt, 1985). As discussed in the preceding pages, *Hexaglottis* (excluding *H. nana*) is believed to be a natural (monophyletic) assemblage distinguished by a number of specialized features, their polarity determined by outgroup comparison and by generally accepted trends in Iridaceae. The characters used for the cladistic analysis are presented in Table 2, and most of them are discussed
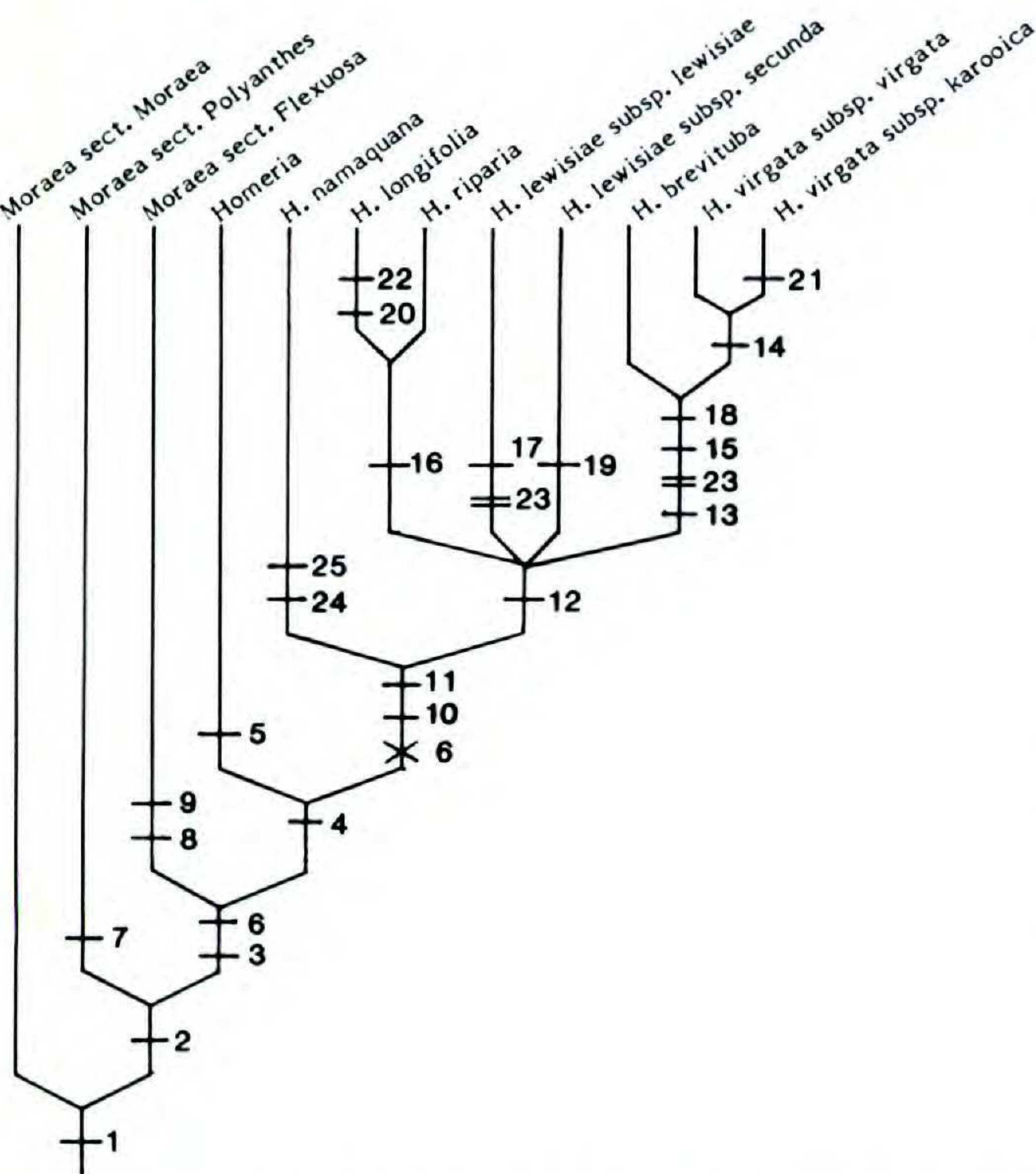
FIGURE 5.   Cladogram of *Hexaglottis* and its relatives in subtribe Homeriinae indicating the possible phylogeny of the genus and of the species within *Hexaglottis*. The characters (synapomorphies) are listed in Table 2. Character states evolved independently (parallelisms) are indicated by double lines and a probable reversal by a cross.

in more detail in the pages dealing with morphology and cytology of *Hexaglottis*. The basic structure of the *Moraea* flower and the reduction and specialization in *Homeria* and some species of *Moraea* have been discussed at length elsewhere (Goldblatt, 1980, 1986). Reasons for considering $x = 10$ the basic chromosome number in *Moraea* and its allies have been presented in two studies (Goldblatt, 1971b, 1976a) dealing primarily with chromosome cytology.

The immediate sister group of *Hexaglottis* is probably *Homeria,* and the genera share a series of derived and reduced floral features as well as the same chromosome number and karyotype. Their common ancestor is probably a species group in *Moraea,* a genus of some 120 species, from which have been segregated several smaller genera that stand out phenotypically in a variety of unusual features. A study in progress suggests that each of these segregates is related to a species or section of *Moraea. Homeria* and *Hexaglottis* together are probably related to *M. flexuosa* of the monotypic section *Flexuosa,* in turn most likely derived from species at present placed in section *Moraea.* The sole synapomorphy that

TABLE 2.   Characters used in the cladogram (Fig. 5), the derived (apomorphic) state listed first, followed by the presumed ancestral (plesiomorphic) condition.

1. Corm tunics composed of hard, wiry, blackish fibers forming an open reticulum—tunics composed of straw-colored fibers forming a fine reticulum.
2. Basic chromosome number $x = 6$—basic number $x = 10$.
3. Karyotype comprising only acrocentric chromosomes—karyotype comprising submetacentric pairs as well as acrocentrics.
4. Style branches narrow and not petaloid—style branches broad and petaloid.
5. Nectaries and nectar guides present on inner and outer tepals—nectaries and nectar guides present on outer tepals only.
6. Filaments united entirely (or free near the apex)—filaments united in the lower half.
7. Flowers shades of blue to violet—flowers shades of yellow.
8. Stem flexuose—stem more or less straight.
9. Tepal claws longer than the limbs—tepal claws about as long as or shorter than the limbs.
10. Style branches divided to the base—style branches forked apically, usually above the stigma lobe.
11. Arms of the style branches filiform, apically stigmatic—arms of the style (if present) flat and curving outwards.
12. Lateral rhipidia sessile and enclosed in the sheathing bracts—lateral rhipidia borne on discrete stalks exceeding the subtending bracts.
13. Hypanthium tube present, at least 1 mm long—tepals free from the base.
14. Hypanthium tube at least 3 mm long—tube 1–2 mm long.
15. Ovary enclosed in the spathes—ovary exserted from the spathes.
16. Capsule narrowly obovoid to clavate-truncate—capsule ellipsoid.
17. Capsule more or less cylindric-trigonous—capsule ellipsoid.
18. Capsule elongate-ellipsoid and enclosed in the spathes—capsule ellipsoid and exserted.
19. Capsule beaked—capsule not beaked.
20. Plants polyploid ($2n = 24$)—plants diploid ($2n = 12$).
21. Basic chromosome number $x = 7$—basic number $x = 6$.
22. Plants self-compatible and autogamous—plants self-incompatible.
23. Seeds angular-fusiform—seeds broadly angular.
24. Leaves spreading and undulate—leaves ascending to erect and more or less straight.
25. Leaf margins undulate to lightly crisped—leaf margins straight.

unites these species is the corm tunic which consists of coarse, dark brown to black, netted fibers. Within the group with coarse black corm tunics, *Hexaglottis, Homeria, Moraea* section *Flexuosa*, and *Moraea* section *Polyanthes* appear to form a monophyletic alliance that shares the derived basic chromosome number of $x = 6$ and a karyotype of predominantly to exclusively acrocentric chromosomes. Section *Polyanthes* has blue flowers, an apomorphic character in *Moraea*, and some subacrocentric chromosomes, while *Hexaglottis* and *Homeria* have flowers with nectar guides on both inner and outer tepals and have style branches reduced from the basic petaloid condition. The species of section *Moraea* belonging to this alliance include *M. namaquamontana, M. serpentina, M. tortilis,* and their close allies, all except *M. namaquamontana* being united by having included ovaries and capsules. The detailed relationships of the species in section *Moraea* are not dealt with further and will be the subject of a future study.

Hexaglottis itself stands out in having specialized style branches and having a possible reversal in the filaments being free in the upper half (see discussion under Flower in the section dealing with Morphology). *Hexaglottis namaquana* stands out in the genus as unspecialized and taxonomically isolated. It is probably close to the ancestor of the genus and, given its very local distribution, must be regarded as a relict species. It is the sister species to the other species of the genus, which all have sessile lateral rhipidia, an important synapomorphy in *Hexaglottis*. The included ovary and hypanthium tube are synapomorphies uniting *H. brevifolia* and *H. virgata,* the latter distinguished by its longer tube and particularly short pedicel. *Hexaglottis virgata* subsp. *karooica* has unusually large flowers (probably a specialized condition but not reflected in the cladogram) and the derived chromosome number of $2n = 14$. *Hexaglottis riparia* and *H. longifolia* form another species pair, linked by the derived capsule shape. *Hexaglottis longifolia* stands out here in having large capsules, autogamous reproduction, and in being polyploid. The two subspecies of *H. lewisiae* apparently share no synapomorphy, or at least none that I have been able to identify. However, they are too similar morphologically to be regarded as separate species. Further study may throw more light on their relationship and will perhaps indicate the presence of specialized features linking them.

The parallelism shared by *Hexaglottis lewisiae* subsp. *lewisiae* and the *H. virgata–H. brevituba* clade, narrow fusiform seeds (character 23), suggests a possible alternative phylogeny with these taxa forming a single clade. This is an attractive hypothesis, suggesting as it does the derivation of the species with a perianth tube and cylindric, included ovary (i.e., *H. virgata* and *H. brevituba*) from an ancestor like subsp. *lewisiae,* which at least has an unusually narrow ovary. The separation of *H. lewisiae* subsp. *secunda* from subsp. *lewisiae* that would result from such an interpretation is difficult to accept given their otherwise similar morphology.

One significant conclusion that is evident from the cladistic analysis is that *Moraea* as presently defined is shown to be paraphyletic, consisting of a number of discrete lineages, some of which are treated as distinct genera. The analysis of the relationships of the main species groups in the whole alliance is in progress and there will likely be some changes to the taxonomy of *Moraea* and its segregates. Such changes may include *Hexaglottis* but it seems preferable, nevertheless, to publish the revision according to the present taxonomy. The species, *H. nana,* is not reassigned to any genus, as this would be premature given the prevailing uncertainty about the relationships of species in *Moraea* itself.

SYSTEMATIC TREATMENT

Hexaglottis Ventenat, Decades Generum Novorum 6, no. 3. 1808. TYPE SPECIES: *H. longifolia* (Jacq.) Salisb., lectotype, designated by Lewis (1959: 219–222).

Important references: Baker, Handbook Irid. 75–76. 1892 et Flora Cap. 6: 31–32. 1896; Lewis, Flora Cape Peninsula 225. 1950; J. S. African Bot. 25: 215–230. 1959.

? *Plantia* Herbert, Edwards Bot. Reg. 30: Misc. 89. 1844. TYPE SPECIES: *P. flava* Herb. [The identity of *P. flava*, treated by Lewis (1959) as conspecific with *H. virgata*, is uncertain. No type material is known. The protologue seems to match *Hexaglottis* and single-leafed species of *Homeria* sections *Homeria* and *Conanthera* equally well. *Plantia* is cited here as doubtfully congeneric with *Hexaglottis*.]

Plants variable in size, 12–120 cm high. *Corm* globose, ± symmetric, 10–20 mm diam. or larger if surrounded by accumulated tunic layers, the tunics consisting of dark brown to blackish layers of thick vertical ribs connected by fine cross-

fibers, the older layers increasingly fibrous and dissected. *Leaves* usually 2–3, occasionally only 1, linear, usually ascending and longer than the stems, often trailing distally, or ± prostrate, flat or channeled, usually inserted towards stem base or at some distance above the ground, the margins plane or undulate. *Stem* erect, straight to slightly flexuose, branched, with only one main axis or with 2–6 diverging secondary axes; lateral rhipidia (inflorescence units) either stalked on short branches (*H. namaquana*) or sessile and partly enclosed by the subtending stem bract, this usually as long or longer than spathes. *Rhipidia* stalked (*H. namaquana*) or sessile except the terminal, 2–several-flowered; *spathes* herbaceous, or partly to entirely dry and pale at flowering time, attenuate, except in *H. namaquana,* the outer often concealed by the sheathing stem bracts and membranous below, ½–⅔ as long as the inner (subequal in the lateral rhipidia of *H. longifolia*); in sessile rhipidia the upper part of inner visible above bracts except in *H. longifolia. Flowers* stellate, upright or facing sidewards, yellow, scented or not, the nectar guides deeper yellow and usually surrounded by small dark spots, larger on the outer tepals, located near the base of the limbs, the tepals free or united below as a closed tube; *perianth tube* (when present) cylindric, 1–7 mm long, narrow, usually curving slightly outward, partly enclosed in the spathes; *tepals* with short erect claws 1–2 mm long, forming a narrow cup enclosing base of filaments or filament column; the outer slightly larger than the inner and with a small nectary on the claw; limbs extended horizontally, the outer ± ovate to oblong, the inner oblong to cuneate. *Filaments* 4–6 mm long, monadelphous, united for 1–2(–3) mm, weakly diverging above; *anthers* 3–9 mm long, linear, initially erect, curling inwards and partly collapsing after anthesis. *Ovary* narrowly ellipsoid to ± cylindric or wider above, exserted or included in the spathes; *style* dividing at apex of the united part of the filaments into 3 short branches, each divided almost to the base into 2 filiform (microscopically grooved) arms, extending outwards on either side of the subtending filaments, ciliate and stigmatic only at the apex. *Capsule* ellipsoid, obovate to clavate, or ± cylindric, exserted or included in the spathes, usually only 1 per inflorescence in *H. virgata; seeds* angular, sometimes narrowly so. *Basic chromosome number x = 6; diploid numbers 2n = 12, 14, 24.*

Distribution. Winter rainfall parts of southern Africa, from Port Elizabeth in the east, to the Cape Peninsula and north throughout Namaqualand, also locally on the Roggeveld Escarpment in the western Karoo.

KEY TO *HEXAGLOTTIS* AND OTHER AFRICAN IRIDACEAE WITH A *HEXAGLOTTIS*-TYPE FLOWER

1a. Rhipidia 2–several, arranged in a fascicle, each on a short stalk; outer inflorescence spathes usually not entirely sheathing, but with a diverging apex .... '*Hexaglottis*' *nana*
1b. Rhipidia many, not fasciculate but in spicate or racemose arrangement, each either sessile or stalked; outer inflorescence spathes entirely sheathing.
  2a. Lateral rhipidia stalked.
    3a. Flowers blue-violet; style arms 2.5–3 mm long .... *Moraea hexaglottis*
    3b. Flowers yellow; style arms about 4 mm long; leaves comparatively broad and short, to 11 mm wide, spreading on the ground and twisted, the margins undulate and often crisped ....
      .... 1. *H. namaquana*
  2b. Lateral rhipidia sessile, spicately arranged on the main axes.
    4a. Tepals free to base; ovary and capsule partly to well exserted from the spathes.
      5a. Capsules narrowly ellipsoid to cylindric-trigonous; rarely more than 3 mm at the widest point, plants of open and dry habitats .... 2. *H. lewisiae*
      5b. Capsules obovoid to clavate, truncate above; 4–8 mm at the widest point; plants of moist habitats, streamsides, and seeps.
        6a. Capsules 12–16(–23) mm long and 6–8 mm wide; inner spathe of lateral rhipidia usually shorter than outer and concealed by the sheathing bract leaves ... 4. *H. longifolia*
        6b. Capsules 6–10(–12) mm long and ca. 4 mm wide; inner spathe of the lateral rhipidia usually longer than outer and not concealed .... 3. *H. riparia*
    4b. Tepals united into a tube below the claws; ovary and capsule enclosed within the spathes.
      7a. Perianth tube 1–2 mm long; upper part of the ovary often emerging from the spathes; plants of northern Namaqualand and the Richtersveld .... 5. *H. brevituba*
      7b. Perianth tube (3–)4–9 mm long; ovary entirely included; plants of the northwest, western, and southern Cape and western Karoo .... 6. *H. virgata*

1. **Hexaglottis namaquana** Goldbl., sp. nov. TYPE: South Africa. Cape: Namaqualand, top of Spektakel Pass, stony clay soil among patches of quartzite, *Goldblatt 3059* (holotype, MO; isotypes, K, NBG). Figure 6.

Plantae 15–30 cm altae, foliis 2–3 prostratis undulatis, marginibus undulatis vel crispis, omnibus rhipidiis pedunculatis ex bracteis vaginantibus caulium exsertis, tepalis liberis, ca. 2 cm longis, ovario 4–5 mm longo plerumque exserto, capsulis oblongo-ellipsoideis ca. 8–10 mm longis.

Plants 15–30 cm high. *Corm* 1–1.5 cm diam., the tunics fibrous, dark brown to black, extending above into short stiff bristles. *Leaves* 2–3, all ± basal, 8–15 cm long, to 11 mm wide, ± prostrate, irregularly undulate or twisted, the margins undulate or crisped. *Stem* several-branched and all branches (on plants in full bloom) stalked, the branches subtended by dry, sheathing bracts 17–21 mm long. *Rhipidia* stalked, exserted from the subtending bracts; *spathes* herbaceous or becoming dry above, acute, the inner 2.5–3 cm long, the outer about half as long. *Flowers* yellow, stellate with free, spreading tepals; *tepals* about 2 cm long with claws about 2 mm long, the outer tepal limbs to 5 mm wide, the inner narrower. *Filaments* united only at very base (seemingly free), 3–4 mm long; *anthers* about 3 mm long, straight and suberect before dehiscence. *Ovary* 4–5 mm long, usually just exserted from spathes, the style arms spreading, about 4 mm long. *Capsules* narrowly oblong-ellipsoid, 8–10 mm long; *seeds* angular, about 1 mm diam. *Chromosome number* $2n = 12$.

Flowering time. Late September to October; flowers opening in the mid afternoon, after 3:00 P.M. and fading near sunset.

Distribution. *Hexaglottis namaquana* is known only from the eastern slopes of the Spektakelberg, some 16 miles west of Springbok in northern Namaqualand (Fig. 6). It is found towards the top of Spektakel Pass, in hard, stony, clay soil, sometimes covered with white quartzite pebbles of the Nama System. Outcrops of Nama shales and quartzites are rare in Namaqualand, where granites and granitic sands are the rule. *Hexaglottis namaquana* may be found in other parts of Namaqualand where there are similar outcrops of the Nama System. The species is sympatric with *H. lewisiae*, which on Spektakel Pass is a tall slender, narrow-leafed plant, blooming very late in the day. Its flowers open at about 5:30 P.M. and last about three hours. The flowers

of *H. namaquana* open at about 3:00 P.M. and begin to fade at 5:30. They are further isolated reproductively by a shift in flowering season. *Hexaglottis namaquana* blooms from late September into mid October, whereas *H. lewisiae* in this area blooms from mid October to late November.

Diagnosis and relationships. *Hexaglottis namaquana*, discovered only in 1974, is a remarkable member of the genus. It has the small yellow flowers that characterize *Hexaglottis*, but unlike all the other species, the lateral rhipidia are borne on long branches rather than being sessile. The former feature must be regarded as primitive for the genus and separates *H. namaquana* from the other species. Members of this species are fairly short and are unusual also in having the leaves strongly undulate to crisped. The capsule is unspecialized in being well exserted from the spathes and in being ellipsoid. In other species of *Hexaglottis* the capsule is either elongated and sometimes linear or is shortly stalked and enclosed within the spathes.

Additional specimens examined. SOUTH AFRICA. CAPE–29.17 (Springbok): Spektakel Pass, west of Springbok (DA), *Goldblatt 5172* (MO, NBG); rocky eastern slopes near the top of Spektakel Pass, *Goldblatt 6672* (MO).

2. **Hexaglottis lewisiae** Goldbl., J. S. African Bot. 37: 234. 1971. TYPE: South Africa. Cape: *Thunberg s.n.* "*Moraea flexuosa* b" [holotype, Herb. Thunberg 1217, UPS (this is the specimen selected by Lewis, 1959: 224 as the lectotype of the invalid *M. flexuosa*)]. Figure 7.

Moraea flexuosa L. f., Suppl. Pl. 100. 1782; Ker, Bot. Mag. 19: tab. 695. 1803, nom. illeg. superf. pro *Ixia longifolia* Jacq. *Sisyrinchium flexuosum* (L. f.) Spreng., Syst. Veg. 1: 167. 1825, nom. illeg. bas. illeg. *Homeria flexuosa* (L. f.) Sweet, Hort. Brit. 1: 395. 1827, nom. illeg. bas. illeg. *Hexaglottis flexuosa* (L. f.) Sweet, Hort. Brit. ed. 2: 498. 1830; Lewis, J. S. Afr. Bot. 25: 223. 1959 et Fl. Cape Peninsula 225. 1950, nom. illeg. bas. illeg. TYPE: as for *Ixia longifolia* (= *Hexaglottis longifolia*).

Hexaglottis longifolia (Jacq.) Salisb. sensu Baker, Flora Cap. 6: 32. 1896, pro parte (excluding the type of *H. longifolia*).

Homeria spicata (Ker) Sweet sensu Klatt, Linnaea 34: 626. 1866, pro parte [excluding the type of *H. spicata*, this now placed in *Homeria elegans* (Jacq.) Sweet, cf. Goldblatt, 1981: 462–464]. Klatt's (1866) concept of *H. spicata* included *Hexaglottis virgata*, *H. longifolia*, and *H. lewisiae*.
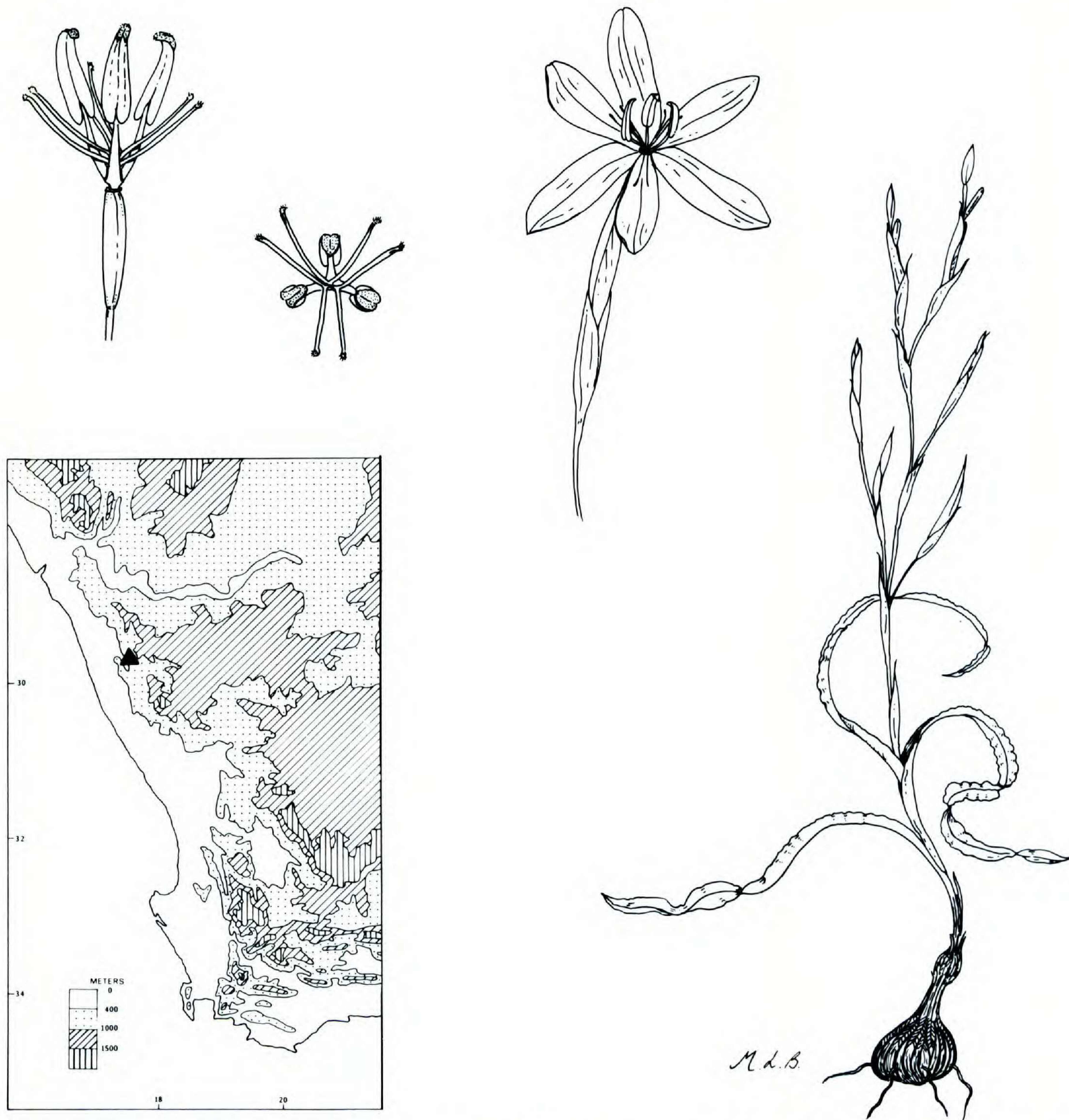
FIGURE 6. Morphology and distribution of *Hexaglottis namaquana.* Habit ×0.5; flower full size; side and top view of the stamens and style branches ×2.

Plants variable in size, (12–)20–60 cm high. *Corm* 15–20 mm diam., symmetric, the tunics (pale–)dark brown, fibrous, occasionally produced upwards into a neck. *Leaves* 1–3(–4), inserted towards the base (sometimes shortly above the ground), ascending, linear, channeled, the margins sometimes inrolled or rarely undulate and the leaves rather short, normally much exceeding the stem and trailing above. *Stem* usually bearing 1–3 secondary branches near the base, often flexuose, the lateral rhipidia sessile, usually overlapping the rhipidium above, subtended by a sheathing stem bract concealing at least the lower part of the spathes, and usually about two-thirds their length. *Rhipidia* sessile except the terminal; *spathes* herbaceous, dry above, (2.5–) 3–4.5 cm long, attenuate, the inner slightly longer than the outer. *Flower* golden yellow with a strong sweet scent, stellate with free tepals, the outer often feathered brownish on the reverse, the nectar guides deeper yellow, usually surrounded by several small dark greenish spots; *tepals* 19–24 mm × 7–10 mm (subsp. *lewisiae*), 24–30 mm × 10–13 mm (subsp. *secunda*), the claws 1.5–2

FIGURE 7.   Morphology of *Hexaglottis lewisiae* subsp. *lewisiae* and the distribution of both subspecies of *H. lewisiae*. Habit, corm, and fruiting branch ×0.5; flower full size; seeds much enlarged.

mm long, the limbs horizontal, the outer ovate, the inner more or less cuneate, about as long to 2 mm shorter than the outer. *Filaments* 4–6 mm long, united for 1–1.5 mm; *anthers* 5–7 mm long before collapsing. *Ovary* (5.5–)6–12 mm long, usually partly to entirely exserted at flowering, rarely entirely included (*Barker 2558*); style about 2 mm long, the style arms spreading and 6–7 mm long. *Capsule* triangular in section and narrowly cylindric, 11–16(–20) mm long (subsp. *lewisiae*) or terete and ellipsoid, 8–13 (–15) mm long (subsp. *secunda*), then often shortly beaked, dehiscing in the upper third to half only; *seeds* angular, sometimes narrowly so and tapering at both ends, 1.2–2 mm long, 0.7–1 mm at the widest, winged in northern populations. *Chromosome number* $2n = 12$.

Flowering time. (September–)October–November; flowers opening between 3:00 and 4:00 P.M. in the south and beginning to fade towards 7:00 P.M., only opening towards sunset in the Namaqualand populations and fading at about 8:00 P.M.

Distribution and biology. Hexaglottis lewisiae is widespread in the southern African winter rainfall area (Fig. 7). It extends from Springbok in the north through the southwestern Cape as far east as the Humansdorp district. It is common only in the western Cape and has a scattered distribution to the north of Piketberg and east of Bredasdorp. It is found in dry and exposed sites, often on stony ground, and occurs on sandy and clay soils.

Like most species of *Hexaglottis*, *H. lewisiae* is pollinated by bees, but pollination has been studied in most detail in this species, and my observations are summarized here. The relatively small and seemingly inconspicuous flowers appear to be very attractive to small bees. When the flowers open in mid afternoon, bees rapidly appear around the plants and begin to gather pollen. They visit the same flowers several times, collecting pollen as soon as it is exposed in the anther sacs, which dehisce slowly from the apex. Pollen is the primary reward and only occasionally is some nectar also taken. The small quantity of nectar produced seems to be of minor interest to the pollinators. Fruit and seed production is very successful in *H. lewisiae*, and plants develop several full capsules from each of the many inflorescences.

Diagnosis and relationships. Hexaglottis lewisiae is a diploid and self-incompatible. Its yellow flowers are almost identical to those of all other species of *Hexaglottis*, except that unlike *H. virgata* and *H. brevituba*, the tepals are free to the base. It shares with all but *H. namaquana* the similar vegetative feature of sessile lateral rhipidia. It is most easily confused with *H. riparia* and *H. longiflora*, but these have obovoid or clavate capsules, thus always broadest in the upper third and markedly flat-topped, unlike the cylindric or ellipsoid, and sometimes beaked, capsules of *H. lewisiae*. Hexaglottis riparia and *H. longifolia* grow in moist situations and, possibly as a consequence, have more and longer leaves than is usual in *H. lewisiae*. The combination of their three or four leaves, obovate-clavate capsules, moist habitats, and sometimes even smaller flowers makes it unlikely that *H. riparia* and *H. longifolia* will be confused with *H. lewisiae*.

History. Hexaglottis lewisiae has been known since the younger Linnaeus (1782) described the species as *Moraea flexuosa* based on material collected by Carl Peter Thunberg a few years earlier. The epithet is regarded today as superfluous and illegitimate since Linnaeus cited as a synonym *Ixia longifolia* Jacq., now *H. longifolia*. The combination *Hexaglottis flexuosa* was made by Sweet in 1830, and the species, usually including *H. longifolia*, was known by this name for several years. The later nineteenth century botanists generally did not recognize *H. flexuosa*. F. W. Klatt included it, together with *H. virgata* and *H. longifolia*, in *Homeria spicata*, this a synonym of *Homeria elegans* (Goldblatt, 1981). Later, Klatt (1882) recognized *Hexaglottis*, including *H. virgata* and *H. longifolia* (presumably but not explicitly including *H. lewisiae*). J. G. Baker (1896) included *H. flexuosa* in *H. longifolia*, and the distinction between the two species was only reestablished by Lewis in 1950. The new name *H. lewisiae* was proposed in 1971 by the present author for the species that until this time was known by the illegitimate name *H. flexuosa*.

Variation. There appear to be two major forms of *Hexaglottis lewisiae*, the southern and typical, treated here as subsp. *lewisiae*, which extends from the western Cape coast eastwards through the southern Cape to Humansdorp. It has medium-sized flowers with tepals 19–24 mm long and distinctive long slender capsules 11–20 mm long that tend to dehisce only in the upper part. The seeds are also comparatively small as a result of the need to be accommodated in the

narrow locules. The karyotype in this form appears to be uniform and consists of four strongly acrocentric chromosome pairs and two acro- to submetacentric pairs.

Populations to the north of the Olifants River mountains, from Clanwilliam north to Springbok, treated as subsp. *secunda,* comprise plants with larger flowers, the tepals 24–30 mm long, somewhat shorter ellipsoid capsules 8–13(–15) mm long, and larger seeds. The chromosome cytology of this series of populations is not as well known, but two Namaqualand populations examined have karyotypes with a large metacentric chromosome pair. This northern form is morphologically variable. Namaqualand plants have a single leaf in the wild, but two leaves in cultivation, and slightly smaller flowers than those from the northwest Cape. The extensive populations from the western Karoo near Nieuwoudtville have capsules with a beaklike apex, a feature weakly developed and often obscure in Namaqualand plants. Capsules in populations from Clanwilliam and Vanrhynsdorp are unknown, and karyotypes have been determined for one northwest Cape population. The flowers of the Namaqualand populations have a different phenology, opening between 5:30 and 6:00 P.M., whereas all other forms of *H. lewisiae* open between 3:00 and 4:00 P.M. and fade at about 6:00 P.M.

KEY TO THE SUBSPECIES OF
HEXAGLOTTIS LEWISIAE

1a. Capsules ellipsoid, 8–13(–15) mm long, often distinctly beaked; outer tepals 24–30 mm long, flowers usually secund .... 2A. subsp. *secunda*
1b. Capsules cylindric or nearly so, 11–16(–20) mm long, not beaked; outer tepals 19–24 mm long, flowers usually upright ....
.... 2B. subsp. *lewisiae*

2A. subsp. **secunda** Goldbl., subsp. nov. TYPE: South Africa. Cape: stony east-facing slopes near the top of Spektakel Pass, west of Springbok, *Goldblatt 6673* (holotype, PRE; isotypes, K, MO, NBG, S, US, WAG).

Planta 30–60 cm alta, floribus usitate secundis tepalis 24–30 mm longis 10–13 mm latis, ovario 5.5–9 mm longis, capsulis ellipsoideis 8–13(–15) mm longis saepe rostratis.

Plants 30–60 cm high. Flowers usually secund; *tepals* 24–30 mm long, 10–13 mm wide. *Ovary* 5.5–9 mm long, usually at least partly exserted at flowering. *Capsule* terete and ellipsoid, 8–13 (–15) mm long, dehiscing for at least half its

length; *seeds* angular, narrowly winged on the ridges, about 2 mm long, ca. 1 mm at the widest.

Distribution. Subspecies *secunda* has a scattered distribution throughout the northwest Cape and Namaqualand. Records extend from Clanwilliam north through the Olifants River Valley to Vanrhynsdorp, to the Karoo north and east of Nieuwoudtville, and into Namaqualand, where it has been recorded west of Garies, in the Kamieskroon district, and on the Spektakelberg, west of Springbok. Plants grow in rocky ground, either in clay soil, as on the Spektakelberg and in the Karoo, or in sand.

Additional specimens examined. SOUTH AFRICA. CAPE–29.17 (Springbok): stony east-facing slopes near the top of Spektakel Pass, west of Springbok (DA), *Goldblatt 6613* (MO).

30.17 (Hondeklipbaai): Klip Vlei, between Kamieskroon and Garies (BD), *Thorne s.n.* (SAM 49973); roadside between Brakdam and Rietkloof, *Pearson 5664* (K); 0.5 km SW of Skuinskraal farm, Hondeklipbaai road (DB), *van Berkel 453* (MO, NBG).

31.18 (Vanrhynsdorp): Zandkraal, sandveld (DB), *Acocks 14826* (K), *Barker 5665* (NBG), *Snijman 889* (MO, NBG); flats below the Gifberg, 12 km south of Vanrhynsdorp, *Goldblatt 6992* (MO, PRE); slopes of the Olifants River Bridge, south of Klawer, rocky sandstone soil (DC), *Goldblatt 6991* (K, MO, NBG, PRE).

31.19 (Calvinia): Loeriesfontein road, ca. 2 miles north of the Waterfall (AC), *Goldblatt 108* (J); karroid hills northeast of the Klip Koppies, Nieuwoudtville, *Goldblatt 7073* (MO); red clay soil among ironstone boulders, Glenlyon farm, Nieuwoudtville, *Goldblatt 6535* (MO); Nieuwoudtville, rocks on top of kopies, *Galpin 11137* (K, PRE).

32.18 (Clanwilliam): 10 km north of Clanwilliam, rocky sandstone soil (BB), *Goldblatt 6990* (MO, PRE, STE, US).

2B. Subsp. **lewisiae.**

Plants (12–)20–60 cm high. Flowers usually upright; *tepals* 19–24 mm long, 7–10 mm wide. *Ovary* 8–10 mm long, usually partly to entirely exserted at flowering, rarely entirely included. *Capsule* terete to triangular in section, narrowly cylindric, 11–15(–20) mm long, dehiscing in the upper third to half only; *seeds* angular-ellipsoid, tapering at both ends, 1.2–1.4 mm long, ca. 0.7 mm at the widest.

Distribution. Subspecies *lewisiae* extends from the Cape west coast east through the southern Cape to Humansdorp. It appears to be common only in the west and records are very scattered east of Bredasdorp. Figure 7.

Specimens examined. SOUTH AFRICA. CAPE–32.18 (Clanwilliam): NE edge of Verlorenvlei (AD–BC), *Pil-*

lans 7803 (BOL); De Hoek, Piketberg (DD), *Barker 2558* (NBG).

33.18 (Cape Town): Mamre hills (AD), *Compton 9828* (NBG); Porterville (BB), *Loubser 466* (NBG); ca. 10 km north of Malmesbury (BC), *Goldblatt 6173* (MO, S, US); mountains around Cape Town (CD), *Ecklon & Zeyher s.n.* (84) (S); foot of Lions Head, *Pappe s.n.* (SAM 70674); Oudekraal, Cape Peninsula, *Goldblatt 163* (J); Bakoven, *Lewis 971* (SAM); Camps Bay, *Moss 13403* (BM); Table Mountain (CD), *Ecklon 536* (BM, K, MO, PRE); Wynberg Hill, *Pillans 10198* (MO, US); Kirstenbosch, *Lewis 672* (NBG, SAM); Kirstenbosch, slopes near the herbarium, *Goldblatt 5104* (MO); Kirstenbosch, near the temporary offices, *Goldblatt 6634* (BR, MO, PRE, WAG); below Pearson House, Kirstenbosch, *Goldblatt 6634* (BR, MO, PRE, WAG); near Bishopscourt, *Salter 9002* (BOL); behind Groot Schuur, *Wolley Dod 360* (BM, BOL, K); Rosebank, *H. Bolus 3801* (BOL, K); Tygerberg Nature Reserve (DC), *Loubser 3059* (MO); Langverwacht, above Kuils River, *Oliver 4803* (K, MO, PRE, STE); Stellenbosch Flats (DD), *Garside 66* (K); between Klapmuts and Paarl, *Acocks 3677* (S); Berg River near Paarl, *Drège s.n.* in 1840 (K, S), *Barker 8797* (NBG).

33.19 (Worcester): Gydo Pass (AB), *Wall 705* (S); Worcester, beim Wasserfall (AC), *Ecklon & Zeyher Irid. 29* (1.11) (LD, MO); near Tulbagh, *Leighton 1317* (BOL); Tulbagh plains, *Marloth 9575* (PRE); Tulbagh Cemetery, *Goldblatt 5224* (MO); Wolseley, *Barker 2072* (NBG); du Toits Kloof (CA), *Stokoe s.n.* (SAM 60126); Worcester Veld Reserve (CB), *Olivier 204* (STE).

33.21 (Ladismith): 5 mi. west of Ladismith (AC), *Rycroft 3030* (NBG).

33.22 (Oudtshoorn): Ruigtevlei, near Swart R., George (DC), *Fourcade 1525* (BOL).

33.24 (Steytlerville): Essenbosch hills (CD), *Fourcade 4420* (K).

34.18 (Simonstown): Simons Bay (AB), *Wright 269* (K); Hout Bay, *Wall s.n.* (S); Noordhoek, *Barker 2728* (BOL, NBG); Bergvliet Farm, *Purcell 124* (SAM).

34.19 (Caledon) Elgin (AA), *Dahlstrand 1164* (PRE); Dwarsberg-Somerset Sneeukop, *Stokoe s.n.* (SAM 55728); Genadendal (AB), *Prior s.n.* (K); between Houw Hoek and Kleinmond (AC), *Werdemann & Oberdieck 678* (B, K, PRE); Hemel en Aarde (AD), *Gillett 90* (STE); 8 mi. from Stanford on the road to Elim, *Gillett 4506* (BOL, K); Klippiesbaai, Vogelklip, Hermanus, *S. Williams 873* (C, MO, WAG); near Napier (BD), *Leipoldt 3551* (BOL); between Baardscheerdersbos and Elim (DA), *Goldblatt 7107* (MO, PRE).

34.22 (Mossel Bay): along the river at Great Brak River (AA), *Young s.n.* (BOL 5541); between George and Great Brak River (?AB), *Burchell 6151* (K).

34.24 (Humansdorp): Oudebosch flats (AA), *Fourcade 960* (BOL).

Without precise locality: Cape of Good Hope (CBS), *Forster s.n.* (BM); *Thunberg s.n.* "*Moraea edulis* Ker," "*Moraea polyanthos*" (S "Herb. Casstrom," "Herb. Swartz"); rock crevices above forest plantation, Clanwilliam, *Galpin s.n.* (BOL).

Introduced: Réunion, Trou aux Cerfs, *Vaughan 3255* (SAM), *Lorence 15764* (K).

3. **Hexaglottis riparia** Goldbl., sp. nov. TYPE: South Africa. Cape: along the Olifants River

at Citrusdal campsite, after fire, *Goldblatt 6706* (holotype, NBG; isotypes, K, MO, PRE, STE). Figure 8.

Hexaglottis longifolia var. *angustifolia* Lewis, J. S. African Bot. 25: 222. 1959, pro parte (excluding the type of var. *angustifolia*, this placed in *H. longifolia* in the present paper).
(*Plantia flava* Herb., Edwards Bot. Reg. 30: misc. 89. 1844 is a possible synonym. See discussion below under History.)

Planta 45–90 cm alta, foliis (2–)3 linearibus, rhipidiis lateralibus sessilibus, bracteis caulis imbricatis longioribus quam internodis, spathis exterioribus usitate in bracteis caulis inclusis, tepalis liberis 16–21 mm longis 6–8 mm latis, ovario 5–7 mm longo exserto, capsulis obovato-clavatis 6–10(–12) mm longis.

Plants 45–90 cm high. *Corm* 13–20 mm diam., the tunics of fine, light brown fibers. *Leaves* (2–)3, linear, 3–5 mm wide, ascending, channeled, the margins incurved, usually bent and trailing above, the lowermost longest, about as long as the stem, the upper decreasing in length and width. *Stem* straight, simple or 1–3-branched from the lower nodes, the lateral rhipidia sessile at each node, subtended by a sheathing stem bract often entirely concealing the inflorescence spathes, these as long or somewhat longer than the internode and overlapping the next bract. *Rhipidia* sessile, except the terminal; *spathes* herbaceous, attenuate, dry apically, 3.3–3.8 cm long, about as long as the subtending stem bract, the outer shorter than the inner, often hidden. *Flowers* stellate with free tepals, deep yellow, strongly scented; *tepals* 16–21 mm long, 6–8 mm wide, with claws about 2 mm long, the limbs spreading, the inner slightly shorter than but as wide as the outer. *Filaments* 4–6 mm long, united for 1.5–2.5 mm; *anthers* 5–6 mm long. *Ovary* 5–7 mm long, exserted; style arms 5–6 mm long, extended horizontally. *Capsules* obovoid-clavate, somewhat truncate, 6–10(–12) mm long, about 4 mm wide; *seeds* angular, 1–1.5 mm long, 1 mm at the widest diam. *Chromosome number 2n = 12.*

Flowering time. October–November; flowers open at about 5:00 P.M. and begin to fade after 7:30 P.M.

Distribution. *Hexaglottis riparia* has a limited range, occurring in valleys of the western Cape mountains between Tulbagh Kloof in the south and Clanwilliam in the north (Fig. 9). It appears to be restricted to streambanks and possibly edges of marshes. Such areas are frequently overgrown with tall vegetation, and *H. riparia* accordingly blooms only after fires or heavy graz-

FIGURE 8. Morphology of *Hexaglottis riparia*. Habit, flowering, and fruiting branches × 0.5; single flower and capsule full size.

ing when the habitat has been opened up considerably.

Diagnosis and relationships. *Hexaglottis riparia* has flowers typical of the genus. It is distinctive largely in its small obovoid to clavate fruits and in its slender, often willowy stems. The capsules are 6–10 mm long, or occasionally in robust plants up to 12 mm. *Hexaglottis longifolia* has similarly shaped capsules but they are much larger, usually 16–23 mm long. The similarity in

capsule shape prompted Lewis (1959) to include the only collection of *H. riparia* known to her in *H. longifolia* var. *angustifolia*. The type of the latter has unusually narrow leaves but in other respects the type corresponds well to typical *H. longifolia*. This species differs further from *H. riparia* in having pale yellow, unscented flowers and in being self-compatible, autogamous, and tetraploid with $2n = 24$. The flowers of *H. riparia* are deep yellow and scented, and, like other members of the genus, it is self-incompatible and diploid with $2n = 12$. The similar capsule shape in *H. riparia* and *H. longifolia*, a derived feature, probably indicates that they are closely related.

History. This species was apparently collected first by Ecklon & Zeyher in the Tulbagh district in the 1820s, and rarely since then. It was initially assigned to *Hexaglottis longifolia* and subsequently cited by Lewis (1959) under *H. longifolia* var. *angustifolia*. There is a possibility that the species described as *Plantia flava* may be the same as *H. riparia*. Baker (1896) and Lewis (1959) treated the monotypic *Plantia* as congeneric with *Hexaglottis*. The type is, however, unknown, and the description is ambiguous and could apply as well to some species of *Homeria* as to *Hexaglottis*. *Plantia flava* was grown and flowered in England from corms collected by George Synnot, who lived in the Clanwilliam district from 1821 to 1825 (Gunn & Codd, 1981). If *Plantia flava* is a species of *Hexaglottis*, it is probably conspecific with *H. riparia*, the only species of *Hexaglottis* in the northwest Cape with capsules that correspond with Herbert's description of the capsules as obovate.

Specimens examined. SOUTH AFRICA. CAPE–32.18 (Clanwilliam): river banks, Clanwilliam (BB), *Galpin 11483* (BM, K, PRE, UPS); Clanwilliam, *Leipoldt 376* (SAM).
32.19 (Wuppertal): along the Olifants river at Citrusdal campsite (CA), *Goldblatt 6555* (K, MO, NBG), *6706* (K, MO, NBG, PRE, STE).
33.19 (Worcester): Worcester, Tulbaghskloof, etc., *Ecklon & Zeyher Irid. 30* (77.9) (K, MO).

4. **Hexaglottis longifolia** (Jacq.) Salisb., Trans. Hort. Soc. 1: 313. 1812; Baker, Flora Cap. 6: 32. 1896, in part excl. *H. lewisiae* (as *H. flexuosa*); Lewis, Flora Cape Peninsula 225. 1950 et J. S. African Bot. 25: 223–225. 1959. *Ixia longifolia* Jacq., Hort. Vindob. 3: 47 & tab. 90. 1776. *Moraea longifolia* (Jacq.) Pers., Syn. Pl. 1: 49. 1805. *Moraea flexuosa* L. f., Suppl. Pl. 100. 1782, nom. illeg. superf. pro

Ixia longifolia Jacq., applied to *H. lewisiae*. *Sisyrinchium flexuosum* (L. f.) Spreng., Syst. Veg. 1: 167. 1825, nom. illeg. bas. illeg. *Homeria flexuosa* (L. f.) Sweet, Hort. Brit. 1: 395. 1827, nom. illeg. bas. illeg. *Hexaglottis flexuosa* (L. f.) Sweet, Hort. Brit. ed. 2: 498. 1830; Lewis, J. S. African Bot. 25: 223. 1959, nom. illeg. bas. illeg., applied to *H. lewisiae*. TYPE: South Africa. Cape: illustration in Hort. Vindob. 3: tab. 90. Figure 9.

Hexaglottis longifolia var. *angustifolia* Lewis, J. S. African Bot. 25: 222. 1959. TYPE: South Africa. Cape: Du Toits Kloof, *Pillans 8436* (BOL, holotype), pro parte (including only the type, other specimens here treated as *H. riparia*).

Plants 60–150(–200) cm high. *Corm* 15–20 mm diam., the tunics of fine, light brown fibers. *Leaves* 3–4(–5), linear, ascending, the lower longest, 50–100 cm long, the upper decreasing in size, 6–12 (–20) mm wide, flat or channeled, usually bent and trailing distally. *Stem* straight, simple or 1–3-branched from the lower nodes; lateral inflorescences sessile at each node, subtended by a sheathing stem bract often entirely concealing the spathes, as long, longer, or shorter than the internode. *Rhipidia* sessile, except the terminal; *spathes* herbaceous, attenuate, dry at apex, 3.5–5.5(–7.5) cm long, the inner about as long as the subtending stem bract, the outer shorter, often hidden. *Flowers* pale yellow, odorless or with a very faint odor, stellate, with free tepals, the nectar guides usually only on the outer tepals, inconspicuous; *tepals* with claws about 2 mm long, the outer with limbs 19–27 mm long, 8–11 mm wide, the inner 16–23 mm long, 6–9 mm wide. *Filaments* 4–6 mm long, united for 2–3 mm; *anthers* 5–6 mm long before anthesis. *Ovary* 8–12 mm long, exserted, the style arms comparatively short, 4–6 mm long, ascending, reaching only to the base of the anthers. *Capsules* well exserted, obovoid-clavate, truncate, 12–16(–23) mm long, 6–8 mm wide, dehiscing for ½–¾ their length; *seeds* angular, 2–2.3 mm long and up to 1.5 mm at the widest. *Chromosome number 2n =* 24.

Flowering time. Mid October–November; flowers opening (2:00–)2:15–2:45 P.M. and beginning to fade ca. 6:00 P.M.

Distribution and biology. *Hexaglottis longifolia* is restricted to the Cape Peninsula and a few valleys in the mountains between Somerset West and Paarl. It grows along streams and in marshes or shady and damp sites (Fig. 9).

It is the only polyploid species in the genus and further unusual in *Hexaglottis* in being self-compatible and normally autogamous. Although the flowers appear to the human eye similar to those of the bee-pollinated *H. lewisiae*, *H. longifolia* is seldom visited by insects. Plants of *H. longifolia* growing a few feet away from *H. lewisiae* are ignored by bees gathering pollen from the latter species. Flowers of *H. longifolia* placed among those of *H. lewisiae* are consistently avoided by bees. Clearly to these insects, the odorless flowers of *H. longifolia* are very different to those of *H. lewisiae*, which are strongly scented. Possibly there are significant differences in ultraviolet patterning as well.

Diagnosis and history. The good illustration of Jacquin's *Ixia longifolia* accompanying the protologue and now regarded as the type of the species corresponds unmistakably to the tall, pale yellow-flowered *Hexaglottis* of damp shady sites on the Cape Peninsula. The painting shows clearly the characteristic pale yellow flowers, six rather short style branches, and the large, obovoid to clavate capsules. Despite this clear illustration, *H. longifolia* has often been associated with the very different *H. lewisiae* (as *H. flexuosa*) (Klatt, 1895; Baker, 1896), which has deep yellow, scented flowers, long style branches, and linear cylindric capsules. Lewis (1959) has explained in detail this historical confusion and has elaborated the several differences between these two quite distinct species. No further discussion seems necessary here.

Lewis (1959) recognized two varieties of *Hexaglottis longifolia* in her revision, the typical, and var. *angustifolia*, the latter distinguished by narrower, stiff, and strongly channeled leaves, shorter spathes, and smaller capsules. Her decision to treat this somewhat smaller form as a variety of *H. longifolia* was evidently based on similarity of general appearance, including the shape of the capsules, which, although smaller, are obovoid and truncate, and by the habitat: moist places along streams and rivers. The type, from du Toits Kloof, seems to me merely a slightly smaller specimen of *H. longifolia* and can be matched in size by some collections from the Cape Peninsula. It does not appear to warrant taxonomic recognition. However, the other collection cited, *Galpin 11483*, from the Olifants River Valley, is a different species treated here as *H. riparia*. It has smaller capsules and the flowers, examined live from this area, are unlike those of *H. lon-*

FIGURE 9. Morphology of *Hexaglottis longifolia* and distribution of *H. longifolia* and *H. riparia*. Habit, flowering and fruiting branches, and corm ×0.5; flower ± full size; seeds much enlarged.

gifolia. They are bright yellow and strongly scented, in both characteristics corresponding better to *H. lewisiae* and in conflict with *H. longifolia* with its pale yellow, scentless flowers. In addition, *H. riparia* is diploid, $2n = 12$, and self-incompatible, in contrast to the tetraploid and autogamous *H. longifolia*.

Specimens examined. SOUTH AFRICA. CAPE–33.18 (Cape Town): Liesbeek River, below Fernwood (CD), *Salter 8973* (NBG), *8775* (NBG, SAM), *8999* (NBG); Kirstenbosch, *Lewis 673* (NBG, PRE, SAM), *Goldblatt 5934* (MO); Kirstenbosch, below Pearson House, *Malan 120* (NBG), *Goldblatt 6635* (K, MO, PRE, WAG); below Fernwood, *Salter 9377* (BM); above Rhodes Drive, *Salter 9354* (BM); Table Mt., east base in damp soil, *Pillans 10262* (BR, MO); Jonkershoek (DD), *Werdermann & Oberdieck 722* (B, K).

33.19 (Worcester): du Toits Kloof (CA), *Pillans 4836* (BOL).

34.18 (Simonstown): Orange Kloof, swamp (AB), *Wolley Dod 3479* (BM, BOL, K, PRE); shady roadside cutting below Constantia Nek on the road to Groot Constantia, *Goldblatt 6640* (MO, PRE, S).

Without precise locality: *Thunberg s.n.* (S "Herb. Casstrom").

5. **Hexaglottis brevituba** Goldbl., sp. nov. TYPE: South Africa. Cape: Richtersveld, Sabiesies, on the road to Cornelsberg, *Viviers s.n.* in 1983 (holotype, NBG; isotypes, K, MO, PRE). Figure 10.

Planta 40–55 cm alta, foliis 2–4, rhipidiis sessilibus, spathis imbricatis longioribus quam internodis, spathis exterioribus ex bracteis caulis exsertis, tepalis infra connatis, tubo 1–2 mm longo, ovario 8–10 mm longo supra ex bracteis exserto, pedicellis 4–10 mm longis.

Plants 40–55 cm high. *Corm* 12–18 mm diam. or larger if surrounded by accumulated tunic layers, the tunics of coarse, dark brown to blackish fibers. *Leaves* 2–4, linear, ascending, longer than the stems and trailing distally, channeled with margins incurved, inserted towards stem base. *Stem* with 1 main axis or with 2–3 diverging secondary axes, straight or rarely slightly flexuose; lateral rhipidia sessile, partly enclosed by the somewhat shorter subtending stem bracts. *Rhipidia* sessile except the terminal, 3–4-flowered; *spathes* herbaceous, or partly to entirely dry and pale at flowering time, attenuate, (20–)25–30 mm long, exserted from the stem bracts, often membranous below, the outer half to two-thirds as long as the inner. *Flowers* stellate, upright or secund, pale yellow, evidently odorless; tepals united below into a short closed tube; *perianth tube* 1–2 mm long, exserted from the spathes; *tepals* 16–19 mm long, the claws about 1 mm long, the limbs extended horizontally, 5–8 mm wide, the outer larger, narrowly ovate, the inner smaller. *Filaments* 3–4 mm long, united for about 1 mm; *anthers* 7–8 mm long. *Ovary* 8–11 mm long, cylindric, often curved outwards, the upper 1 mm narrow and sterile, the apex often exserted from the spathes; pedicel 4–10 mm long, the style arms about 6 mm long. *Capsule* and *seeds* not known. *Chromosome number* $2n = 12$.

Flowering time. September to October; flowers opening mid afternoon and fading after 7:00 P.M.

Distribution. Hexaglottis brevituba is known from only a few sites in central and northern Namaqualand, from Garies to Steinkopf (Fig. 10). There is only a single record from the central part of Namaqualand, at Stinkfontein south of Garies, and other collections are from the Springbok area and north to the Richtersveld, where the type collection was made. *Hexaglottis brevituba* is probably more common than the present record indicates. It is inconspicuous except when in bloom, and the flowers are open for only a few hours in the mid afternoon of a few weeks, usually towards the end of spring.

Diagnosis and relationships. Hexaglottis brevituba is clearly allied to the widespread *H. virgata*, which has similar vegetative and floral morphology but is readily distinguished by its flowers with a well-developed perianth tube some 4–7 mm long and an entirely included ovary with a pedicel 4–6 mm long. In *H. brevituba* the perianth tube is only 1–2 mm long; the ovary is often apically exserted and the pedicel (4–)7–10 mm long.

History. The first record of *Hexaglottis brevituba* was made by Rudolf Schlechter in 1897 and the collection was identified only as *Hexaglottis*. In Lewis's revision of the genus she placed it in *H. virgata* var. *lata*, the type and only other collection being from the Biedouw Valley. A third collection, made by G. J. Lewis near Springbok, was assigned to *H. lewisiae* (as *H. flexuosa*) by Lewis, who did not notice the characteristic short perianth tube in the poorly preserved flowers. The perianth tube can, however, be seen in this collection when buds are examined carefully. The range of the species was substantially extended to the Stinkfontein Mountains in the Richtersveld by Mike Viviers in 1983. This, the only adequate collection of *H. brevituba*, has been selected as the type.

Specimens examined. SOUTH AFRICA. CAPE: 28.16 (Vioolsdrif): Richtersveld, Sabiesies, on the road to Cornelsberg (CA), *Viviers s.n.* (K, MO, NBG, PRE), *1337* (NBG).
29.17 (Springbok): north of Steinkopf, near Kosies road in kloof northeast of Rabas (BA), *Goldblatt 5748* (MO); near Springbok (DB), *Lewis 743* (SAM).
30.18 (Kamiesberg): Stinkfontein (on the Groot Doorn R.) (CC), *Schlechter 114876* (BOL).

6. **Hexaglottis virgata** (Jacq.) Sweet, Hort. Brit. ed. 2: 498. 1830; Baker, Flora Cap. 6: 32. 1896, pro parte; Lewis, Flora Cape Peninsula 225. 1950 et J. S. African Bot. 25: 225. 1959. *Moraea virgata* Jacq., Ic. Pl. Rar. 2: tab. 228. 1791 et Coll. Bot. 3: 194. 1791. *Ixia virgata* (Jacq.) Willd., Sp. Pl., 1: 202. 1798. *Homeria virgata* (Jacq.) Sweet, Hort. Brit. ed. 1: 395. 1827. TYPE: South Africa. Cape: cultivated in Vienna, illustration in Jacq., Ic. Pl. Rar. 2: tab. 228. Figure 11.

Plants variable in size, 12–85 cm high. *Corm* 13–18 mm diam., or larger if surrounded by accumulated tunic layers, the tunics of coarse, dark brown to blackish fibers. *Leaves* usually 2–3, occasionally only 1, rarely 4, linear, ascending, longer than the stems and trailing distally, channeled with margins curving inward, occasionally loosely coiled above, inserted towards the stem base. *Stem* with 1 main axis or with 1–3(–6) fairly
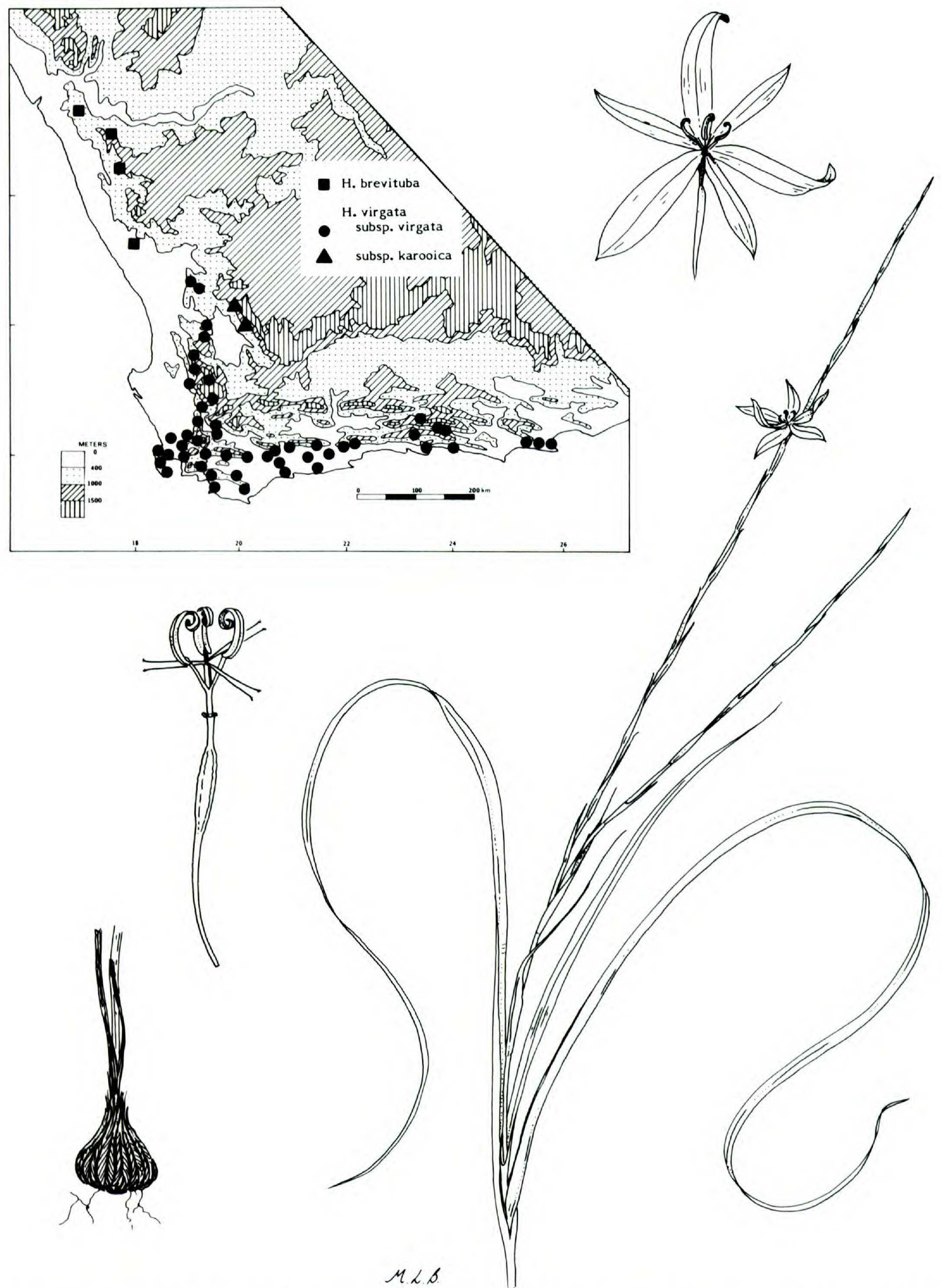
FIGURE 10. Morphology of *Hexaglottis brevituba* and the distribution of *H. brevituba* and *H. virgata*. Habit ×0.5; flower and corm full size; detail of stamens, ovary, and style branches ×2.

long, strongly diverging secondary branches, straight to slightly flexuose, the lateral rhipidia sessile, each partly to almost entirely enclosed by the subtending stem bract, this usually as long or longer than spathes. *Rhipidia* sessile except the terminal, 2–3-flowered; *spathes* herbaceous, or partly to entirely dry and pale at flowering time, attenuate, 22–30(–37) mm long, the outer concealed by a stem bract, often membranous below, ½–⅔ as long as the inner, upper part of the inner extending above the bracts. *Flowers* stellate with the tepals united below into a closed tube, upright or secund, pale yellow, evidently odorless, the nectar guides deeper yellow; *perianth tube* cylindric, narrow, usually slightly curving outward, (3–)4–6(–9) mm long, usually at least partly enclosed in the spathes; *tepals* 14–25 (subsp. *virgata*), 23–32 (subsp. *karooica*) mm long, with short claws 1–1.5 mm long, the limbs extended horizontally, 4–8(–11) mm wide; the outer larger, lanceolate to ovate, the inner smaller, lanceolate to cuneate. *Filaments* 3.3–6 mm long, united for 1–2 mm; *anthers* initially 6–9 mm long. *Ovary* 8–16(–20) mm long, the upper 1–2 mm narrow and sterile, cylindric, included in the spathes, the pedicel short, 5–6 mm long; style arms 5–6 mm long. *Capsule* narrowly spindle-shaped, included in the spathes, 9–13 mm × 2–3 mm (subsp. *virgata*), or 16–22 mm × 4 mm (subsp. *karooica*), only 1 (rarely 2) developed in each rhipidium; *seeds* narrowly angular, 0.7–1 mm wide and 1–2 mm long. *Chromosome number* $2n = 12, 10$ (subsp. *virgata*), or $2n = 14$ (subsp. *karooica*).

Flowering time.   (Late September–)October–December(–mid January); flowers opening 3:00–3:30 P.M. (or up to 4:00 P.M. on cooler days), beginning to fade ca. 6:30 P.M., usually collapsed by 7:00 P.M.

Distribution.   *Hexaglottis virgata* is widespread in the southern African winter rainfall area, extending from the Nieuwoudtville district in the northwest through the western and southern Cape to Port Elizabeth in the east (Fig. 10). It is rather scattered in the west of its range, but common from Malmesbury and the Cape Peninsula eastwards through the southern Cape. It is found more often on heavier soils, particularly shales of the Malmesbury System, but also occurs on granitic substrates. Occasionally *H. virgata* is found on sandy soils of the Cape System. Subspecies *karooica* occurs inland on the Roggeveld

Escarpment, where it favors sheltered and damp situations.

Diagnosis and relationships.   *Hexaglottis virgata* is a distinctive species, unmistakable in its slender, relatively long perianth tube some 4–7 mm in length and very straight stems with strongly diverging lateral branches. The historic confusion about the identity of this species has been due to the poor observation that resulted in overlooking the perianth tube or confusing it with the slender ovary (Lewis, 1959). In fact the upper part of the ovary is narrow, sterile, and tubular, but this is clearly different from the perianth tube from which it is separated by an abscission layer. The only other species of *Hexaglottis* with a perianth tube is *H. brevituba*, described in this paper. *Hexaglottis brevituba* has a much shorter tube, only 1–2 mm long, compared with a tube (3–)4–7 mm long in *H. virgata*. The two species differ in several other features. *Hexaglottis virgata* has an ovary entirely included in the spathes on a short pedicel up to 5 mm long, while *H. brevituba* has a longer pedicel 7–10 mm long, and the ovary is curved and usually just exserted from the spathes.

Two subspecies of *Hexaglottis virgata* are recognized here. The typical and most common, subsp. *virgata*, has relatively small flowers and capsules. It has a wide distribution extending over almost the entire range of the species. Subsp. *karooica*, known only from two isolated sites on the Roggeveld Escarpment, has unusually large flowers, spathes, and capsules.

History.   The earliest existing records of *Hexaglottis virgata* are those made by the Swedish botanists Carl Peter Thunberg and Anders Sparrman in the 1770s, but this common southwestern Cape species must surely have been collected earlier than this. However, it was Nicholas Jacquin who first described the species in 1791, based on plants grown in Vienna, and probably sent to him some years earlier by Franz Boos and Georg Schol, the collectors who provided Jacquin with many of the Cape plants that he illustrated and described. The painting that accompanies the description and serves as the type in the absence of preserved material is excellent and leaves no doubt about the identity of what Jacquin called *Moraea virgata*. After the genera *Homeria* and *Hexaglottis* were recognized as distinct from *Moraea* by E. P. Ventenat in 1808, *M. virgata* was
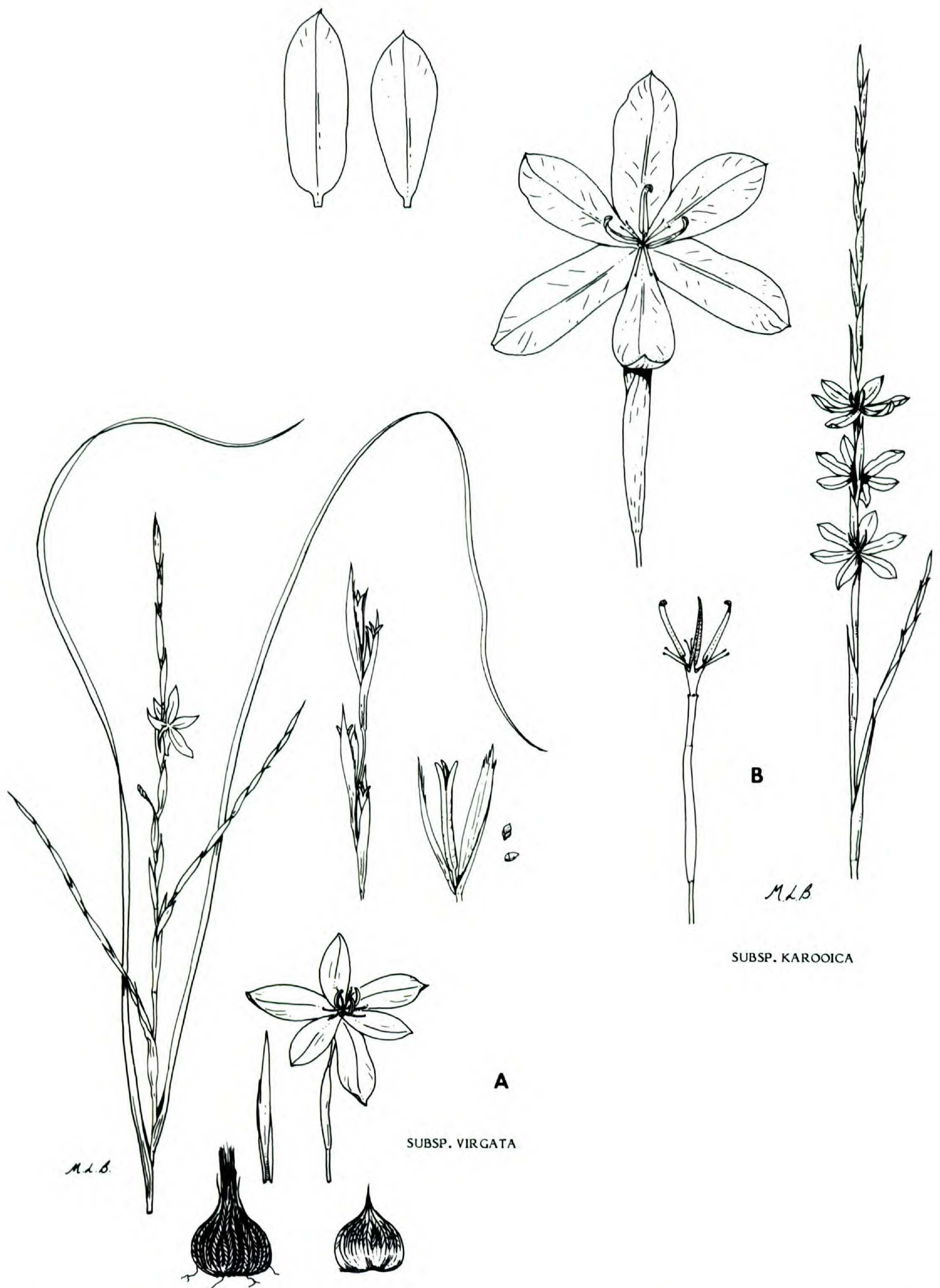
FIGURE 11. Morphology of *Hexaglottis virgata.*—A. Subsp. *virgata.*—B. Subsp. *karooica.* Habits ×0.25; corms ×0.5; flowers, fruiting branch (subsp. *virgata*), separated tepals, and detail (subsp. *karooica*) of androecium and gynoecium full size; single capsule and seeds (subsp. *virgata*) ± ×2.

transferred to *Homeria* (Sweet, 1827) and shortly afterward to *Hexaglottis* (Sweet, 1830). J. G. Baker included *H. lewisiae* (as *H. flexuosa*) and *H. longifolia* in *H. virgata* in *Flora Capensis* (1896). This unsatisfactory treatment was corrected by G. J. Lewis in 1950.

KEY TO THE SUBSPECIES OF
HEXAGLOTTIS VIRGATA

1a. Outer tepals 14–22(–25) mm long × 5–7 (–11) mm wide; spathes (at least the terminal) 22–28(–32) mm long; foliage leaves 1–3, rarely more .... 6A. subsp. *virgata*
1b. Outer tepals 23–32 mm long × 7–10.5 mm wide; spathes (at least the terminal) 32–37 mm long; foliage leaves (2–)3–5 .... 6B. subsp. *karooica*

6A. Subsp. virgata. Figure 11A.

Hexaglottis virgata var. *lata* G. Lewis, J. S. African Bot. 25: 228–229. 1959. TYPE: South Africa. Cape: Welbedacht, Bidouw Valley, *Lewis 2514* (holotype, SAM 61821; isotypes, BOL, PRE, SAM).

Plants 12–50(–70) mm high. *Leaves* 1–3(–4). *Spathes* 22–28(–32) mm long. *Flowers* with perianth tube (3–)4–5.5(–7) mm long; *tepals* 14–22(–25) mm long. *Filaments* 3.3–6 mm long; *anthers* 5–8 mm long. *Ovary* 8–12 mm long; *capsules* 9–13 mm long. *Chromosome number* 2n = 12, 10.

Distribution. The distribution of subsp. *virgata* is the same as that for the species, except that it does not occur on the Roggeveld Escarpment (Fig. 10).

Variation. As circumscribed here, subsp. *virgata* includes the variety *lata*, described by G. J. Lewis for somewhat larger-flowered plants with comparatively wide tepals, from the Biedouw Valley. When this was described in 1959, no other population of *H. virgata* was known from the northwestern Cape, and only one was known from Namaqualand, a poorly preserved specimen, which Lewis included in var. *lata* despite the distorted flowers that could not be accurately measured. *Hexaglottis virgata* is now known from several sites in the northwest Cape, from the Olifants River Valley and adjacent Pakhuis Mountains to the Nieuwoudtville Escarpment. Variation in flower dimensions in these populations is considerable and covers the whole range from typical rather small-flowered subsp. *virgata* (tepals 14–20 × 5–8 mm; spathes 22–28 mm long), which occurs in the Cape Peninsula and southern Cape, to the type of var. *lata* and very similar plants from Nieuwoudtville (tepals 20–25 × 9–

11; spathes 23–30 mm long). The rationale for recognition of the variety has thus disappeared. These northwestern populations do, however, appear to represent a distinct race. Plants from two populations from the northwestern area have a karyotype with strongly acrocentric chromosomes (Fig. 3F) that contrast with the presence of acrocentrics and submetacentrics in the most common southern cytotype (Fig. 3E).

Populations examined from the Cape Peninsula have *n* = 5, and a very different karyotype from those with *n* = 6 (Fig. 3G) (see discussion under Cytology). There seems to be no corresponding morphological difference in the Cape Peninsula plants.

Specimens examined. SOUTH AFRICA. CAPE–31.19 (Calvinia): Grasberg road northwest of Nieuwoudtville, renosterveld (AC), *Goldblatt 7071* (K, MO, NBG, PRE, US); 2–3 km from Nieuwoudtville on the north side of the road to the escarpment, *Goldblatt 7411* (MO); 8 km south of Nieuwoudtville on sandstone slopes, *Goldblatt 7395* (MO).
32.18 (Clanwilliam): 10 km south of Clanwilliam, clay road bank (BB), *Goldblatt 6705* (MO, PRE); 12 km south of Clanwilliam, stony clay bank, *Goldblatt 6989* (K, MO, NBG, PRE, WAG); clay hillside just south of the Alpha turnoff, on the National Road to Citrusdal (BD), *Goldblatt 3028* (MO).
32.19 (Wuppertal): between Doorn River and Bidouw Valley turnoff, stony clay (AA), *Goldblatt 5941* (MO); Welbedacht, Bidouw Valley, *Lewis 2514* (BOL, PRE, SAM).
33.18 (Cape Town): Table Mountain (CD), *Tyson 2488* (SAM), *Bayliss 3054* (UC); kloof between Lions Head and Table Mountain, *Burchell 252* (K); slopes of Devils Peak, above de Waal Drive, Cape Town, *Goldblatt 6717* (MO); near Bishopscourt, *Salter 9001* (BOL); Wynberg Hill, *Pillans 10819* (MO, UPS), *Salter 8978* (SAM), *9545* (BM); Signal Hill, *Lewis 665* (SAM), *Goldblatt 71* (J), *6747* (MO, S), *6748* (MO), *Marloth 7234* (PRE); Camps Bay, *Moss 13403* (J); Observatory grounds, *Davis s.n.* (SAM 61050); Tygerberg Nature Reserve (DC), *Loubser 3004* (MO); Stellenbosch (DD), *Boucher 3392* (PRE, STE); 4 miles from Faure on the Stellenbosch road, *Lewis 2340* (SAM); Groot Drakenstein und fuss Paarlberg, *Drège s.n.* (S).
33.19 (Worcester): farm Waterval, near Porterville (AA), *Loubser 966* (NBG); Tulbagh Cemetery (AC), *Goldblatt 5225* (K, MO, S); 9 miles along the Leeuwfontein road (AD), *Pearson 3508* (K); Bains Kloof (CA), *Schlechter 9106* (BM, BOL, BR, G, K, MO, PRE, S), *2597* (PRE); 8 miles west of Worcester, near the Breede R. (CB), *Lewis 5309* (NBG, PRE); Karoo Garden, Worcester, *Compton 17849* (NBG), *Lewis 5304* (NBG); Pokkraal, Rawsonville, *le Roux s.n.* (PRE); between Worcester and Robertson (DA–DB), *Zinn s.n.* (SAM 65673).
33.20 (Montagu): pasture below 10 O'Clock Mt., Swellendam (CD), *Wurts 486* (NBG).
33.21 (Ladismith): south entrance to Attaquas Kloof (DD), *Thompson 1636* (PRE); Attaquaskloof, Mossel Bay, *Barker 7692* (NBG).

33.23 (Willowmore): hills near Uniondale (CA), *H. Bolus 2484* (K); Prince Alfreds Pass (CC), *Wall 18* (LD); near Misgund (CD), *Goldblatt 6792* (MO); between Misgund and Nieuweplaats (DC), *Fourcade 5485* (PRE, STE); Kliprivier, Tsitsikamma Park, *Bower 625* (PRE); hills near Joubertina (DD), *Fourcade 2374* (BOL, K); Joubertina, Bokkeveld hill, *Esterhuysen 6772* (BOL).

33.25 (Port Elizabeth): Van Staadens Hoogte (CC), *MacOwan 2055* (BM, K); Greenbushes (CD), *Holland 4051* (BOL); Baakens River Valley, Port Elizabeth (DC), *Olivier 1739* (WAG); Port Elizabeth, *Long 502* (K), *Paterson sub Rogers 2414* (J).

34.18 (Simonstown): Steenberg (AB), *Compton 1665* (NBG); Bergvliet, *Purcell s.n.* (BOL 1638, SAM), *124* (SAM); Somerset West, on stiff clay soil (BB), *Parker 4388* (BOL, K, MO, NBG).

34.19 (Caledon): Houw Hoek (AA), *Penther 572* (K, S); Greyton-Genadendal (AB), *Lindeberg s.n.* (S); Napier Ruggens (BD), *Marloth 10006* (PRE); between Napier and Bredasdorp (CA), *Goldblatt 6937* (MO); Franskraal, along the coast above the beach (CD), *Goldblatt 5368* (MO); sandy soil on slopes near Avoca (DA), *Goldblatt 6939* (MO, PRE, S, WAG); Bredasdorp Poort (DB), *Esterhuysen 19580* (BOL).

34.20 (Bredasdorp): Storms Vlei Kloof (AA), *Leipoldt 3549A* (BOL); Bontebok Park, Swellendam (AB), *Liebenberg 6710* (STE); Zuurbraak (BA), *Barker 5029* (NBG); Grootvadersbos, paths in wood (BB), *Willems 88* (NBG); shale hills west of Heidelberg, *Goldblatt 7416* (MO); Potteberg (BC), *David s.n.* (NBG); Malgas, Swellendam distr., *Leipoldt 3550* (BOL).

34.21 (Riversdale): hill top 5 km west of Riversdale (AA), *Goldblatt 5436* (MO); Still Bay, limestone hills (AD), *Esterhuysen 19538* (BOL, PRE); limestone hills south of Albertinia, Stilbaai road on turnoff to Riethuiskraal, *Goldblatt 7428* (MO); Onverwacht, Albertinia (BA), *Muir 1207* (BOL).

34.23 (Knysna): Plettenberg Bay (AB), *Rogers 28241* (K), *26762* (K).

Without precise locality: CBS, *Alexander s.n.* (BM, K); *Sparrman s.n. Iris edulis* (S); *Thunberg s.n. Iris edulis* (S).

6B. Subsp. karooica Goldbl., subsp. nov. TYPE: South Africa. Cape: eastern border of farm Blomfontein, 22 km from Middelpos towards de Hoop, *Snijman 765* (holotype, NBG; isotypes, K, MO, PRE). Figure 11B.

Planta robusta, 30–85 cm alta, foliis (2–)4–5, spathis 32–37 mm longis, tubo perianthii 6.5–9 mm longo, tepalis 23–32 mm longis, 7–11 mm latis, antheris 6–8 mm longis, capsulis 16–22 mm longis.

Plants robust and 30–85 cm high. *Leaves* usually 4–5, rarely 2–3. *Spathes* 32–37 mm long. *Flowers* with perianth tube 6.5–9 mm long; *tepals* 23–32 mm long, 7–11 mm wide. *Filaments* 4–6 mm long; *anthers* 6–8 mm long. *Ovary* 15–20 mm long. *Capsules* 16–22 mm long. *Chromosome number* 2n = 14.

Distribution. Subsp. *karooica* is known from two widely separated localities along the Rog-

geveld Escarpment, near Blomfontein west of Middelpos in the north, and on the slopes of Sneeukrans on the farm Voelfontein northwest of Sutherland, some 50 km to the south. The habitat at both sites is moist, the plants growing among large rocks near seepage zones.

Variation. The subspecies is variable in flower size. Plants from the Middelpos area have very large tepals 28–32 mm long while those from Voelfontein have smaller flowers with the tepals somewhat narrower and only 23–24 mm long. Despite this variation, other features, including large spathes and capsules, higher leaf number, and the unusual karyotype with 2n = 14, in both populations indicate that subsp. *karooica* is indeed a distinct geographical variant of *Hexaglottis virgata*.

Specimens examined. SOUTH AFRICA. CAPE–31.20 (Williston): Roggeveld Escarpment, 71 km SE of Calvinia on Middelpos road via Blomfontein (CC), *Goldblatt 4612* (MO, NBG); eastern border of farm Blomfontein, 22 km from Middelpos towards de Hoop, *Snijman 765* (K, MO, NBG, PRE).
32.20 (Sutherland): Roggeveld, Sneeukrans south of Voelfontein farm, ca. 4,500 ft., in wet site (AD), *Goldblatt 6336* (MO), *7126* (MO).

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